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# Introgression of genes for quantitative traits into oat populations

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INTROGRESSION OF GENES FOR QUANTITATIVE
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# INTRODUCTION

It has been suggested that the high level of adaptation present in today's crop varieties has been attained at the cost of a serious loss of genetic variability. Furthermore, unplanned introduction and inadequate sampling may have limited the germ plasm which plant breeders have used and exploited.

The purpose of this study was to estimate means and genetic variability among segregates from hybrid combinations between Corn Belt oat varieties and exotic lines. The crosses were made in various combinations and in single, three-way, and more complex crosses to provide information for knowledgeable planning of a breeding program designed to increase the quantity of useful variability in oat breeding populations.

# LITERATURE REVIEW

Based on the plant breeding experience at Svalöf, MacKey (1963) states "As time goes on, and the goal put up will come closer, the variability of the material will, however, decrease and consequently the degree of progress is bound gradually to diminish." Simmonds (1962), Harlan (1956, 1966), and Allard and Hansche (1964) express the same idea in reviews related to the subject of variability in plant breeding materials.

Brown (1965) suggests that the problem of reduced variability may be even greater in corn than in small grain breeding programs because small grain breeders have introduced more germplasm in order to add disease resistance to their material.

Wide crosses increase genetic variability rapidly according to Harlan (1966), but very wide crosses frequently result in sterility, physiological unbalance and developmental disturbances which decrease their usefulness. He points out that the one feature common to the evolution of all cultivated plants is the alternate subdivision of the population into subunits and subsequent hybridization among members of the different subunits. He suggests that the most successful cultigens are likely to be those with genotypes with most buffering for the addition of alien germ plasm, and that the amount of differentiation that is permissible before hybridization is related to the degree of buffering. Polyploidy and heterozygosity are examples of such buffering systems. He advocates that plant breeders use all germplasm within genetic reach.

The strategy of wide crosses, especially to permit occupation of new niches or new territories, seems to be widely occurring in natural populations. Documentation is provided by Anderson (1949, 1953) for the extensiveness of such strategy. The common occurrence of wide crosses can be recognized by methods developed by Anderson (1957), to identify variability as specifically resulting from such a cross. Anderson and Hubricht (1938) coined the term, "introgressive hybridization" to denote the gradual infiltration of the germ plasm of one species into that of another as a consequence of hybridization and repeated backcrossing.

Anderson recognized the necessity of a new habitat for variants from such species hybrids. This concept is emphasized in "Hybridization of the Habitat" (Anderson, 1948). A new habitat which results from man's activities frequently provides the requisite niches for hybrids of sympatric species, while geological events such as glaciation, inundation, or reduced rainfall and subsequent recession, drainage, or increased rainfall may provide both the isolation required for species differentiation, and, later, the virgin territory for occupation by introgressants resulting from crosses of allopatric species.

An example of the putative role of introgression in the evolution of an important cultigen is provided by the story of corn. Mangelsdorf, MacNeish, and Galinat (1964) suggest that introgression of *Tripsacum* and teosinte into corn germplasm have played an important role in the improvement of corn after its cultivation began. From a summary of the supposed ancestry of modern corn and teosinte, Galinat, Chaganti, and Hager (1964) suggest that *Tripsacum* may have originated from hybridization of wild corn and *Manisuris*. However, Weatherwax and Randolph (1955) support the view that *Tripsacum*, teosinte and corn all derived from a common ancestor by mutation and selection.

Kihara (1954) summarized the relationships among *Aegilops* diploids and polyploids based on his work since 1918. He used diploid species as "analyzers" to establish genomic relationships. In polyploids one genome remained relatively constant, as evidenced by pairing relationships, while associated genomes were rather highly modified. Species were grouped with a common constant genome. The constant genome shared by a number of polyploids and one diploid acted as a buffer to facilitate gene exchange among unshared genomes of the group according to Zohary and Feldman (1962). The relatively free gene exchange could result in combinations of characters in tetraploids that could not be explained on the basis of the characteristics of only two diploid species, and the enrichment of the gene pools permitted colonization of wider areas by the polyploids than by the diploid parents. Feldman, (1965) and Pazy and Zohary (1965) present evidence, based on field observations of cytology, pollen fertility and seed set, in putative $F_1$ and backcross progenies and artificially derived counterparts, that support the argument for gene flow among the tetraploids. Male sterility can serve to canalize backcrossing in these naturally autogamous species according to Vardi and Zohary (1967), who described introgression from diploid to tetraploid species by way of the triploid $F_1$.

Use was made of wide crosses between Aegilops and Triticum groups by Sears (1956) to incorporate rust resistance from diploid Aegilops umbellulata to hexaploid cultivated wheat. Transfer of rust resistance from diploid and tetrapolid Avena species to the cultivated hexaploid has been described by Sadanaga and Simons (1960).

MacKey (1963) pointed out that in crosses of elite adapted varieties and exotic lines, segregates tend to be inferior to the adapted parent. To circumvent this difficulty, Allard and Hansche, (1964) and Harlan (1956) suggested combining adapted and exotic varieties into a mass reservoir allowing recombination and natural selection. Harlan (1966) summarized the favorable results obtained with this system, and cited the composite crosses of barley and the many varieties they have spawned as such an example. Favorable results have also been reported by Goodman (1965) using exotic maize varieties. Suneson (1945) utilized male sterility to reduce the resources required to make the various crosses.

In a series of studies of natural populations summarized by Allard, Jain, and Workman (1968), estimation of amount of outcrossing, heterozygote advantage, and between and within family genetic variances, have shown that even in autogamous species sufficient recombination occurs to account for the success of such a system. For example, in _A. fatua_ outcrossing at seven sites ranged from 1 to 12% and selective values for the homozygote ranged from 0.28 to 0.64 depending upon the marker used in the estimate (Imam and Allard 1965). Jain and Allard (1960) concluded that heterozygote advantage was necessary to account for the level of heterozygosity found in a closed population of barley.

Harlan and Pope (1922) suggested the use of backcrossing for the transfer of relatively simply inherited characters to commercial varieties. They pointed out the genetical logic of such a program and recognized the probable effectiveness for breaking up unfavorable linkages. Briggs (1935) discussed the expectations for percentage of homozygosity with selfing and backcrossing, and pointed out the expected higher frequency of recovery of the recurrent parent type with this breeding method.

Briggs, (1938) Suneson, Riddle and Briggs (1941), and Suneson (1947) showed comparisons of standard and backcross-improved varieties for certain characters of agronomic importance, and concluded that the expectations were fulfilled for recovery of the recurrent parent type. Suneson (1947) did mention certain small, but real, differences, such as better baking quality of Baart and slightly higher protein in Baart 38. He also enumerated cases where selections from Baart 38 included purple straw, light red seeds, and stripe-rust resistance, and where selections from Federation 41 had superior winter hardiness and mildew resistance. These instances indicated some genetic variability remained in backcross derived varieties.

Briggs and Allard (1953) summarized the requirements for a satisfactory backcrossing program. They suggested using several independent series of backcrosses, with subsequent selection and compositing of the better lines from each program for improving characters controlled by many genes with minor effects. Leininger and Frey (1962) have shown that, while means of backcross populations for heading date, plant height and weight-per-volume regressed toward the recurrent parent value, the rate could not be explained on the basis of additive gene action. The mean for yield showed no indication of returning to the recurrent parent value.

Variances estimated were erratic, but in general, were reduced by additional backcrossing.

Harlan, Martini, and Stevens (1940) suggested a system of combining germplasm of several divergent varieties by convergent crossing. MacKey (1963) presented a modification of this scheme by crossing the $F_1$ of an adapted x unadapted cross to an adapted variety before starting the convergent crossing. He stated "the intention of breeding becomes more and more restorative in favor of the already gained genic constellation while recombination is equally dependent on both parents".

# MATERIALS AND METHODS

My study consisted of two experiments grown in replicated randomized complete block designs at Ames, Iowa, in 1967 and 1968. Each plot was a hill of 32 seeds, planted with a jab planter, and hills were spaced 30 cm apart perpendicularly, (Frey, 1965). Eight and seven replicates were planted in 1967 and 1968 respectively. Plant heights and heading dates were recorded on two replicates in each year, and these two replicates were not harvested for yield measurements. At maturity the plants in each plot of the remaining six to five replicates (in 1967 and 1968, respectively) were harvested at ground level, placed in a paper bag and stored to dry. Prior to threshing, the bundle of plants from a hill was weighed, then the bundle was threshed and the grain was weighed. Next, the grain weight was subtracted from bundle weight to obtain straw weight.

For each trait, a conventional analysis of variance was computed and the entry sum of squares was partitioned to give estimates of the genetic variances among lines within crosses. Estimates of genetic variance within a cross were made by subtracting the error mean square from the within cross mean square and dividing by the number of replicates used in measuring the trait. Standard errors of the variance estimates were calculated by the formula:

$$\frac{2}{r^2}\left[\frac{(MS_1)^2}{df + 2} + \frac{(MS_2)^2}{df + 2}\right]^{\frac{1}{2}} .$$

A list of the parents used for making the crosses tested in 1967, with a characterization of each, is given in Table 1, and a list of the exact crosses tested and the number of lines tested from each is given in Table 2. Tables 3 and 4 provide similar information for the parents and crosses, respectively, tested in 1968. The classification of varieties as adapted or exotic is somewhat arbitrary, and is based on observations of persons working on the Iowa Agricultural Experiment Station oat project. It does, however, furnish a classification method for grouping several crosses together for statistical summary and interpretation.

In 1968 the "exotic" varieties were introduced from outside the North American continent, and "semi-exotic" varieties were from North America, but are not acceptable as standard varieties in Iowa. Parents which are not acceptable as standard varieties in Iowa were called "unadapted" in 1967.

As used herein, an oat "line" is an $F_2$-derived line tested in the $F_4$, i.e., it is a bulk progeny from a single $F_2$ plant. In more complex crosses it is a bulk progeny from a single $S_2$ plant tested in the $S_4$. To obtain a sufficient quantity of seed to sow seven or eight plots to a line, I

Table 1. Parents of oat crosses tested in 1967

| Name and classification of varieties | Cereal index or plant introduction number | Parentage | Source of unadapted varieties |
|---|---|---|---|
| <u>Adapted</u> | | | |
| Bonkee | | (Bonham$^5$ x Cherokee$^3$ -R.L. 2105) (Bonham$^3$ x Cherokee$^3$ -R.L. 2105) | |
| C 237-89 | CI 7970 | Clintland x Garry 5 | |
| C 237-93 | | Clintland x Garry 5 | |
| C 649 | CI 7550 | (Clintland$^8$ x R.L. 2105) (Clintland$^7$ x R.L. 2105) | |
| Clintland | CI 6701 | Clinton$^4$ x Landhafer | |
| Clinton | CI 3971 | Bond x D69 | |
| Goodfield | CI 7266 | Clintland (Garry x Hawkeye-Victoria) | |
| Newton | CI 6642 | Nemaha (Clinton x Boone-Cartier) | |
| Tippecanoe | CI 7680 | Clintland 60$^2$ x Mo 0-205 | |
| <u>Unadapted</u> | | | |
| C 750 | | Burnett x CI 5545 | Iowa |
| C 753 | | Nemaha x CI 5545 | Iowa |
| Ceirch du Bach | CI 2923 | | Wales |
| $F_2$ of 12 | CI 4636 | | Minnesota |
| Napped Argent | | | France |
| Selecta | | | |
| DL 41372 | PI 185783 | | Argentina |
| | PI 267989 | *Avena sterilis* | |
| | CI 5545 | Appler (Clinton$^2$ x Sante Fe) | |
| 13-11 | | | France |

Table 2. Oat crosses and number of lines from each tested in 1967

| Crosses | Number of lines tested |
|---|---|
| Clintland x PI 185783 | 50 |
| Bonkee (Clintland x PI 185783) | 50 |
| Newton x CI 4636 | 50 |
| Bonkee (Newton x CI 4636) | 50 |
| | |
| Clinton x PI 267989 | 40 |
| CI 7555 (Clinton x PI 267989) | 50 |
| CI $7555^2$ (Clinton x PI 267989) | 50 |
| CI $7555^3$ (Clinton x PI 267989) | 50 |
| | |
| CI 7555 x CI 2923 | 50 |
| CI $7555^2$ x CI 2923 | 50 |
| CI $7555^4$ x CI 2923 | 50 |
| CI $7555^6$ x CI 2923 | 50 |
| | |
| Napped Argent x CI 5545 | 50 |
| Goodfield (Napped Argent x CI 5545) | 50 |
| Napped Argent x C 750 | 50 |
| Goodfield (Napped Argent x C 750) | 50 |
| Goodfield x C 750 | 50 |
| | |
| CI 7970 x CI 5545 | 50 |
| CI 7970 x C 753 | 50 |
| C 750 x CI 5545 | 50 |
| CI 7970 (C 750 x CI 5545) | 50 |
| | |
| C 237-93 x 13-11 | 50 |
| CI 7970 (13-11 x C 753) | 50 |
| | |
| Goodfield x Tippecanoe | 50 |
| CI 7555 x Newton | 40 |
| Andrew x Burnett | 30 |

Table 3. Parents of oat crosses tested in 1968

| Name and classification of varieties | Cereal index or plant introduction number | Parentage | Source of exotic and semi exotic varieties |
|---|---|---|---|
| Adapted | | | |
| Beedee | CI 6752 | Beacon (Hawkeye x Victoria) | |
| Bonham | CI 4676 | Bond x D 69 | |
| Burnett | CI 6573 | Colo (Victoria x Hajira-Banner) | |
| C 237-89 | CI 7970 | Clintland x Garry 5 | |
| Cherokee | CI 3846 | Bond x D 69 | |
| Clarion | CI 5647 | Clinton x Marion | |
| Clintland | CI 6701 | Clinton$^4$ x Landhafer | |
| Clintland 60 | | | |
| Goodfield | CI 7266 | Clintland (Garry x Hawkeye-Victoria) | |
| Marion | CI 3247 | Markton x Rainbow | |
| Newton | CI 6642 | Nemaha (Clinton x Boone-Cartier) | |
| Tippecanoe | CI 7680 | Clintland 60$^2$ x Mo 0 205 | |
| Semi-exotic | | | |
| Abegweit | CI 4970 | Vanguard x Erban | Canada |
| Columbia Clinton | CI 5630 | Columbia x Clinton | Illinois |
| LMHJ | CI 6914 | Landhafer (Mindo x Hajira-Joanette) | Florida |
| Sturdy | CI 5117 | Coker x Victoria-Richland | South Carolina |
| Exotic | | | |
| Pusa Hybrid X27 | CI 3442 | | India |
| Tedere No. 277 | CI 3270 | | Italy |
| SA 15 | PI 244473 | | Brazil |

Table 4. Oat crosses tested in 1968

| Single crosses | Three-way crosses |
|---|---|
| Adapted by exotic crosses | Adapted (adapted x exotic) |
| CI 7970 x Tedere | CI 7970 (Goodfield x Tedere) |
| Goodfield x Tedere | CI 7970 (Tippecanoe x Tedere) |
| Tippecanoe x Tedere | Goodfield$^{2}$ x Tedere |
| | |
| CI 7970 x Pusa Hybrid | CI 7970 (Goodfield x Pusa Hybrid) |
| Goodfield x Pusa Hybrid | CI 7970 (Tippecanoe x Pusa Hybrid) |
| Tippecanoe x Pusa Hybrid | Goodfield (CI 7970 x Pusa Hybrid) |
| | Tippecanoe (Goodfield x Pusa Hybrid) |
| | |
| CI 7970 x SA 15 | CI 7970 (Goodfield x SA 15) |
| Goodfield x SA 15 | Goodfield (Tippecanoe x SA 15) |
| Tippecanoe x SA 15 | Tippecanoe (CI 7970 x SA 15) |
| | |
| Adapted x semi-exotic | Adapted (adapted x semi-exotic) |
| CI 7970 x Abegweit | CI 7970 (Tippecanoe x Abegweit) |
| Goodfield x Abegweit | Goodfield (CI 7970 x Abegweit) |
| Tippecanoe x Abegweit | Tippecanoe (Goodfield x Abegweit) |
| | |
| CI 7970 x Columbia-Clinton | CI 7970 (Goodfield x Columbia-Clinton) |
| Goodfield x Columbia-Clinton | Goodfield (CI 7970 x Columbia-Clinton) |
| Tippecanoe x Columbia-Clinton | Tippecanoe (CI 7970 x Columbia Clinton) |
| | Tippecanoe (Goodfield) x Columbia-Clinton) |
| | |
| CI 7970 x LMHJ | Goodfield (CI 7970 x LMHJ) |
| | Tippecanoe (CI 7970 x LMHJ) |
| | |
| CI 7970 x Sturdy | Goodfield (CI 7970 x Sturdy) |
| | Tippecanoe (CI 7970 x Sturdy) |

Table 4 (Continued)

| Single crosses | Three-way crosses |
| --- | --- |
| Adapted x adapted | |
| Goodfield x Tippecanoe | |
| Bonham x Clarion | |
| Clintland x Newton | |
| Clintland 60 x Marion | |
| Burnett x Cherokee | |
| Clintland 60 x Beedee | |

had to grow an $F_3$ panicle row (1 m long) to increase the seed supply of each line. Therefore, the seeds used to plant the replicated experiments were in $F_4$. Parental lines were also progenies of single seeds. In 1967, the number of lines tested from each cross varied (see Table 2), but in 1968, 48 lines were tested from each. Five lines were tested from each parent in 1967 and six lines from each in 1968. In several cases, data were not available from the exact parents used in the crosses being tested. I did not sow Andrew, Burnett, C 750 or Clinton in 1967. CI 7555, an isoline of Clinton, was used to estimate performance values for the latter variety, C 753 was used to represent C 750, and mid-parent values for the Andrew x Burnett cross were not estimated from parental data. I had to bulk seeds from several lines to have a sufficient quantity to make an entry of Napped Argent, C 753, 13-11 and CI 5545 in 1967, since these varieties were poor seed producers. All lines within crosses were selected at random, except in the Clinton x PI 267989 cross, where I restricted selection to non-shattering types. One restriction that I had to impose in using a line was that a headrow of it had produced enough seed to plant the required number of replicates. Ten standard varieties were included in the test each year to serve as a base for judging the general level of performance for each experiment. I included one entry of each standard variety in 1967 and three of each in 1968.

Single-degree-of-freedom comparisons were made of actual cross means with expected means based on parental values. Since a sample of parental lines was not included with each cross these comparisons were not orthogonal. Expected means were calculated as a weighted average of the means of the parent lines which made up the cross, e.g. $1/2\ (P_1 + P_2)$ for a single cross, and $1/2\ P_3 + 1/4\ (P_1 + P_2)$ for a three-way cross.

# RESULTS

## Relation of Cross Means to Parental Values

Means of parental varieties for heading date, plant height and grain and straw weight are shown in Tables 5 and 6 for parents tested in 1967 and 1968, respectively, and means for the check varieties are shown in Table 7 for comparison.

When crosses were grouped according to types (i.e., adapted x exotic, adapted x semi-exotic, etc.), expected means for traits, calculated from parental data, were reasonably reliable for predicting actual cross means for the materials grown in 1968 (Table 8). By groups of crosses, deviations from expected values for heading date ranged from 0 days for adapted x adapted crosses to 1.1 days earlier for adapted x exotic crosses; for plant height from 0 cm for adapted x exotic crosses to 2 cm taller for adapted (adapted x exotic) and adapted (adapted x semi-exotic); for grain weight from 1 g per plot less for adapted x exotic to 2 g per plot more for adapted (adapted x exotic); and for straw weight from 1 g per plot less for adapted x exotic to 4 g per plot more for adapted (adapted x semi-exotic). The general tendency for means of heading dates to be earlier and plant heights to be taller may be due to a bias in the manner in which measurements were made. The sample of

Table 5. Means and notation of presence or absence of genetic variance for parents of oat crosses tested in 1967

| Parent | Heading date (June) | Plant height (cm) | Grain weight (g/plot) | Straw weight (g/plot) |
|---|---|---|---|---|
| PI 185783 | 26.7 | 97 | 33* | 68* |
| CI 2923 | 42.9* | 115* | 8* | 80* |
| Napped Argent | 22.9 | 97 | 26* | 57* |
| 13-11 | 29.7 | 91* | 20 | 56 |
| PI 267989 | 25.0 | 87 | 13 | 47* |
| CI 4636 | 20.9* | 96 | 23* | 56* |
| CI 5545 | 18.0 | 78 | 18 | 34 |
| C 753-19 | 16.6 | 85 | 13 | 32 |
| Bonkee | 14.1 | 88 | 25 | 42 |
| Goodfield | 14.7 | 82 | 24 | 41 |
| Tippecanoe | 14.7 | 85 | 26 | 47 |
| CI 7970 | 12.6 | 87 | 23* | 34 |
| Clintland | 16.1 | 98 | 32* | 52 |
| Newton | 14.2 | 87 | 23 | 42 |

*Genetic variance indicated as significant by F test.

Table 5 (Continued)

| Parent | Heading date (June) | Plant height (cm) | Grain weight (g/plot) | Straw weight (g/plot) |
|---|---|---|---|---|
| CI 7555 | 16.8 | 100 | 38 | 59 |
| C 237-93 | 22* | 99* | 34* | 55* |

Table 6. Means and notation of presence or absence of genetic variance for parents of oat crosses tested in 1968

| Parent | Heading date (June) | Plant height (cm) | Grain weight (g/plot) | Straw weight (g/plot) |
|---|---|---|---|---|
| Tedere #277 | 20.5* | 91 | 23 | 50 |
| Pusa Hybrid | 6.9 | 60 | 10 | 26 |
| SA 15 | 19.9* | 86* | 32* | 73* |
| Abegweit | 16.0* | 80 | 29 | 49 |
| Columbia-Clinton | 18.4 | 88 | 32 | 66* |
| LMHJ | 16.6 | 71 | 33 | 64 |
| Sturdy | 15.9 | 73 | 27 | 62 |
| CI 7970 | 12.6 | 77 | 26* | 47 |
| Goodfield | 16.3 | 74 | 23 | 51 |
| Tippecanoe | 14.1 | 79 | 26 | 54 |
| Bonham | 14.2 | 82 | 34 | 61* |
| Clarion | 18.6 | 88 | 40 | 75* |
| Beedee | 19.3 | 88 | 32 | 64 |
| Clintland 60 | 16.9 | 84 | 30 | 58 |
| Clintland | 15.8 | 86 | 29 | 60 |
| Newton | 14.8 | 77 | 26* | 57 |
| Marion | 16.8 | 88 | 35 | 68 |
| Burnett | 15.2 | 83 | 40* | 69 |
| Cherokee | 13.8 | 75 | 27 | 56 |

*Genetic variance indicated as significant by F test.

Table 7. Means of check varieties of oats in 1967 and 1968

| Variety | Heading date (June) 1967 | Heading date (June) 1968 | Plant height (cm) 1967 | Plant height (cm) 1968 | Grain weight (g/plot) 1967 | Grain weight (g/plot) 1968 | Straw weight (g/plot) 1967 | Straw weight (g/plot) 1968 |
|---|---|---|---|---|---|---|---|---|
| Jaycee | 12.0 | 13.8 | 79 | 71 | 25 | 24 | 36 | 45 |
| Clintford | 14.0 | 13.7 | 81 | 75 | 29 | 28 | 48 | 58 |
| X-299-187-6 | 14.0 | 15.0 | 93 | 78 | 33 | 32 | 52 | 54 |
| Nodaway | 15.0 | 14.2 | 96 | 85 | 32 | 33 | 59 | 64 |
| Stormont | 15.0 | 16.2 | 84 | 76 | 29 | 26 | 52 | 61 |
| C-929-13 | 16.0 | 17.0 | 98 | 82 | 32 | 29 | 51 | 60 |
| Garland | 17.0 | 16.7 | 93 | 81 | 33 | 31 | 49 | 57 |
| Portal | 17.5 | 19.0 | 97 | 86 | 36 | 37 | 51 | 68 |
| Burnett | 14.5 | | 97 | | 36 | | 58 | |
| Dawn | | 14.8 | | 91 | | 31 | | 56 |
| O'Brien | | 15.5 | | 89 | | 31 | | 58 |
| Lodi | 18.0 | | 105 | | 35 | | 57 | |
| Mean of check varieties | 15.3 | 15.6 | 92 | 81 | 32 | 30 | 51 | 58 |

Table 8. Actual means and deviations of actual from expected means (based on parental variety performance) for heading date, plant height, grain weight and straw weight by types of crosses tested in 1968

| Type of cross | Number of crosses | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|---|
| | | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| Adapted x exotic | 9 | 14.0 | -1.1 | 78 | 0 | 22 | -1 | 49 | -1 |
| (Adapted x exotic) adapted | 10 | 14.1 | -0.4 | 78 | 2 | 24 | 0 | 51 | 2 |
| Adapted x semi-exotic | 8 | 15.0 | -0.4 | 80 | 1 | 28 | 0 | 56 | 2 |
| (Adapted x semi-exotic) adapted | 11 | 14.7 | -0.3 | 79 | 2 | 28 | 2 | 57 | 4 |
| Adapted x adapted | 6 | 16.1 | 0.0 | 83 | 1 | 31 | 0 | 62 | 1 |
| All crosses | 44 | 14.7 | -0.4 | 79 | 1 | 26 | 0 | 55 | 2 |

[a]dev=actual-expected mean.

plants in a plot represented an $F_2$-derived line, and therefore, was often phenotypically heterogenous. The early and tall plants in a plot were more conspicuous, and in attempting to assign a single plot value, the conspicuous plants may have had undue influence on my estimations.

Yield of grain was greater for each group of three-way crosses, relative to its expected yield, than for the corresponding group of single crosses. The average yield for adapted x exotic single crosses was 1 g per plot less than the expected value and was equal to the expected value for the corresponding three-way crosses, whereas the yield of the adapted x semi-exotic crosses was equal to the expected value and 2 g per plot greater than expected for the corresponding group of three-way crosses.

In Table 9, I grouped the 1968 single and three-way crosses according to the specific exotic or semi-exotic parent used. There are two quite sharp features in this summary: (a) for grain yield, the actual means of three-way crosses tended to be above the expected ones, whereas, for single crosses there was no similar tendency, and (b) a given exotic or semi-exotic variety tended to have similar effects across traits and in both single and three-way crosses. The actual yields of the single crosses were 96 and 100 percent of the expected yields for the exotic and semi-exotic parents, respectively, and 100 and 108 percent,

Table 9. Actual means and deviations of actual from expected means (based on parental variety performance) for heading date, plant height, grain weight, and straw weight, classified by exotic and semi-exotic parents varieties used in the single and three-way crosses tested in 1968

| Parent | Number of crosses | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|---|
| | | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| <u>Single crosses</u> | | | | | | | | | |
| Tedere | 3 | 16.8 | -0.6 | 85 | 1 | 22 | -2 | 50 | -1 |
| Pusa Hybrid | 3 | 11.8 | 1.2 | 70 | 2 | 18 | 1 | 42 | 4 |
| SA 15 | 3 | 13.5 | -3.6 | 78 | -3 | 27 | -1 | 56 | -6 |
| Abegweit | 3 | 15.3 | 0.1 | 80 | 2 | 27 | 0 | 53 | 3 |
| Columbia-Clinton | 3 | 15.2 | -1.2 | 81 | -1 | 30 | 2 | 59 | 1 |
| LMHJ | 1 | 13.1 | -1.5 | 79 | 5 | 25 | -4 | 52 | -4 |
| Sturdy | 1 | 13.8 | -0.5 | 77 | 2 | 26 | 0 | 61 | 7 |
| Adapted x adapted | 6 | 16.1 | 0 | 83 | 1 | 31 | 0 | 62 | 1 |
| <u>Three-way crosses</u> | | | | | | | | | |
| Tedere | 3 | 15.9 | 0 | 81 | 2 | 25 | 1 | 52 | 2 |
| Pusa Hybrid | 4 | 12.8 | 0.4 | 76 | 4 | 22 | 1 | 48 | 4 |
| SA 15 | 3 | 14.1 | -1.6 | 77 | -2 | 26 | 0 | 53 | -3 |
| Abegweit | 3 | 13.9 | -0.9 | 78 | 1 | 27 | 1 | 52 | 2 |
| Columbia-Clinton | 4 | 16.0 | 0.6 | 82 | 3 | 30 | 3 | 62 | 7 |
| LMHJ | 2 | 14.3 | -0.6 | 77 | 2 | 27 | 0 | 56 | 2 |
| Sturdy | 2 | 13.8 | -0.9 | 75 | -1 | 26 | 1 | 55 | 2 |

[a]dev=actual-expected mean.

respectively, for the three-way crosses. Three, two, and two of the exotic parental groups produced mean yields inferior to, no different from, and superior to, respectively, the corresponding expected means for the single crosses. In contrast, five of seven produced superior deviations in three-way crosses. SA 15 tended to be an inferior parent. The means of its single crosses were 3.6 days earlier, 3 cm shorter, 1 g lighter in grain weight, and 6 g lighter in straw weight than the expected means, and for its three-way crosses, the actual means were 1.6 days earlier, 2 cm shorter, and 3 g lighter in straw weight than the expected means. The one single cross with LMHJ produced inferior means, but they were as expected in the three-way crosses that involved this parent. The means of Pusa Hybrid single and three-way crosses deviated positively from the expected values for all traits. The means for Pusa Hybrid single crosses were 1.2 days later, 2 cm taller, and 1 and 4 g heavier in grain and straw weights, respectively, than expected, and the three-way cross means were 0.4 days later, 4 cm taller, and 1 and 4 g heavier in grain and straw weights, respectively, than expected. With the Columbia-Clinton entry, the observed and expected values were similar for the single crosses, but this was the most superior variety when judged on means of three-way crosses. Means of its three-way crosses were 0.6 days later, 3 cm taller, and

3 and 7 g heavier in grain and straw yield, respectively, than the expected means. Tedere, Abegweit, and Sturdy crosses produced trait means that did not deviate much from expected values.

I have shown actual means of crosses and deviations from means expected on the basis of parental performance for the single crosses tested in 1968 in Table 10. In Tables 10, 11, and 12 where there are shown deviations from expected means for individual crosses, significance of the deviations has been indicated. Although data are presented for all traits in these tables, I will discuss heading date and grain yield as illustrative of simply and complexly inherited traits, respectively. I showed earlier that the different exotic and semi-exotic parents may have different prepotencies in crosses, and that a given parent may have different prepotencies in single and three-way crosses. Data in Tables 10 and 11 are arranged to reflect whether cross means were due to a general effect of the exotic or semi-exotic variety, or to specific interactions of the exotic or semi-exotic lines with the various adapted varieties. The mean heading date for the CI 7970 x Abegweit cross was 1.6 days later, and for Goodfield x Abegweit 1.7 days earlier, than expected. None of the other semi-exotic or exotic parents produced mean heading dates significantly earlier and later than expected, but the magnitudes of the

Table 10. Actual means and deviations of actual from expected means (based on parental variety performance) for heading date, plant height, grain weight, and straw weight for single crosses tested in 1968

| Cross | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|
| | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| CI 7970 x Tedere | 14.7 | -1.8** | 86 | 2.2* | 21 | -3.1** | 46 | -3.0* |
| Goodfield x Tedere | 18.0 | -0.4 | 84 | 2.0 | 19 | -4.0** | 50 | -0.7 |
| Tippecanoe x Tedere | 17.7 | 0.4 | 86 | 0.7 | 26 | 1.4* | 56 | 3.6* |
| CI 7970 x Pusa Hybrid | 11.5 | 1.8** | 73 | 4.9** | 19 | 1.7* | 43 | 6.8** |
| Goodfield x Pusa Hybrid | 12.7 | 1.0** | 68 | 1.0 | 18 | 1.7* | 39 | 0.6 |
| Tippecanoe x Pusa Hybrid | 11.4 | 0.9** | 69 | 0.0 | 16 | -1.4 | 44 | 4.4** |
| CI 7970 x SA 15 | 12.5 | -3.7** | 79 | -2.5* | 28 | -0.4 | 56 | -3.6* |
| Goodfield x SA 15 | 15.7 | -2.5** | 78 | -1.9 | 26 | -1.8* | 55 | -7.3** |
| Tippecanoe x SA 15 | 12.2 | -4.8** | 77 | -5.9** | 27 | -1.7* | 57 | -6.8** |
| CI 7970 x Abegweit | 15.9 | 1.6** | 84 | 5.7** | 29 | 1.6* | 51 | 3.3* |
| Goodfield x Abegweit | 14.5 | -1.7** | 75 | -1.7 | 26 | -1.6* | 52 | 1.7 |
| Tippecanoe x Abegweit | 15.4 | 0.4 | 81 | 1.6 | 28 | 0.9 | 57 | 5.7** |
| CI 7970 x Columbia-Clinton | 13.1 | -2.5** | 79 | -3.1** | 28 | -1.1 | 52 | -4.7** |
| Goodfield x Columbia-Clinton | 16.5 | -0.9** | 80 | -0.8 | 29 | 1.4* | 59 | 0.3 |
| Tippecanoe x Columbia-Clinton | 16.0 | -0.2 | 85 | 1.3 | 33 | 3.9** | 65 | 5.2** |
| CI 7970 x LMHJ | 13.1 | -1.5** | 79 | 4.7** | 25 | -3.6** | 52 | -3.6* |

[a] dev=actual-expected mean.

*Actual and expected means differ at .05 level.

**Actual and expected means differ at .01 level.

Table 10 (Continued)

| Cross | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|
| | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| CI 7970 x Sturdy | 13.8 | -0.5* | 77 | 1.6 | 26 | 0.0 | 61 | 6.7** |
| Goodfield x Tippecanoe | 15.7 | 0.5* | 77 | 0.8 | 27 | 3.0** | 57 | 4.8** |
| Bonham x Clarion | 15.4 | -1.0** | 84 | -1.1 | 30 | -6.5** | 63 | -4.8** |
| Clintland x Newton | 16.9 | 1.7** | 85 | 3.3** | 29 | 1.7* | 65 | 5.8** |
| Clintland 60 x Marion | 16.1 | -0.7** | 88 | 2.1* | 32 | -1.0 | 61 | -1.5 |
| Burnett x Cherokee | 15.0 | 0.5* | 81 | 1.9 | 37 | 4.0** | 65 | 2.2 |
| Clintland 60 x Beedee | 17.6 | -0.5* | 86 | 0.3 | 30 | -0.3 | 63 | 1.5 |

Table 11. Actual means and deviations of actual from expected means (based on parental variety performance) for heading date, plant height, grain weight, and straw weight for three-way crosses tested in 1968

| Cross | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|
| | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| CI 7970 (Goodfield x Tedere) | 13.2 | -2.3** | 79 | -0.3 | 24 | -0.5 | 44 | -4.7** |
| CI 7970 (Tippecanoe x Tedere) | 16.6 | 1.7** | 81 | 0.6 | 26 | 0.9 | 56 | 6.2** |
| Goodfield$^2$ x Tedere | 18.0 | 0.7** | 83 | 4.8** | 27 | 4.0** | 58 | 6.7** |
| CI 7970 (Goodfield x Pusa Hybrid) | 13.8 | 1.7** | 78 | 6.8** | 25 | 3.9** | 49 | 6.2** |
| CI 7970 (Tippecanoe x Pusa Hybrid) | 12.9 | 1.3** | 73 | 0.1 | 20 | -1.2 | 43 | 0.2 |
| Goodfield (CI 7970 x Pusa Hybrid) | 13.1 | 0.1 | 79 | 7.9** | 23 | 2.6** | 50 | 6.3** |
| Tippecanoe (Goodfield x Pusa Hybrid) | 11.4 | -1.5** | 73 | 0.6 | 21 | -0.2 | 48 | 1.9 |
| CI 7970 (Goodfield x SA 15) | 14.0 | -1.3** | 79 | 0.5 | 27 | 1.0 | 51 | 3.2* |
| Goodfield (Tippecanoe x SA 15) | 15.0 | -1.7** | 73 | 5.1** | 24 | -1.6** | 52 | -5.3** |
| Tippecanoe (CI 7970 x SA 15) | 13.3 | -1.9** | 78 | -1.8 | 27 | -0.6 | 57 | -0.3 |

[a]dev=actual-expected mean.

*Actual and expected mean differ at .05 level.

**Actual and expected mean differ at .01 level.

Table 11 (Continued)

| Cross | Heading date (June) | | Plant height (cm) | | Grain weight | | Straw weight | |
|---|---|---|---|---|---|---|---|---|
| | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| CI 7970 (Tippecanoe x Abegweit) | 14.2 | 0.4 | 78 | 0.3 | 29 | 2.5** | 51 | 2.0 |
| Goodfield (CI 7970 x Abegweit) | 13.0 | -2.3** | 75 | -0.7 | 25 | -0.4 | 51 | 1.1 |
| Tippecanoe (Goodfield x Abegweit) | 14.7 | -0.5* | 79 | 0.7 | 28 | 2.5** | 56 | 3.6** |
| CI 7970 (Goodfield x Columbia-Clinton) | 14.4 | -0.6** | 80 | 1.0 | 29 | 2.2** | 54 | 1.8 |
| Goodfield (CI 7970 x Columbia-Clinton) | 16.0 | 0.1 | 80 | 2.1* | 28 | 2.6** | 56 | 1.8 |
| Tippecanoe (CI 7970 x Columbia-Clinton) | 17.8 | 3.0** | 88 | 6.9** | 31 | 4.1** | 72 | 17.1** |
| Tippecanoe (Goodfield x Columbia-Clinton) | 16.0 | 0.2 | 81 | 1.4 | 31 | 4.3** | 64 | 7.3** |
| Goodfield (CI 7970 x LMHJ) | 14.7 | -0.7** | 75 | 1.7 | 24 | -1.5* | 51 | -2.2 |
| Tippecanoe (CI 7970 x LMHJ) | 13.9 | -0.5* | 78 | 1.8* | 29 | 1.2 | 61 | 5.9** |
| Goodfield (CI 7970 x Sturdy) | 14.2 | -1.1** | 73 | -1.7 | 25 | 0.8 | 53 | 0.4 |
| Tippecanoe (CI 7970 x Sturdy) | 13.4 | -0.8** | 78 | 0.9 | 27 | 0.8 | 57 | 2.3 |

Table 12. Actual means and deviations of actual from expected means (based on parental variety performance) for heading date, plant height, grain weight, and straw weight for crosses tested in 1967

| Cross | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|
| | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| Clintland x PI 185783 | 17.2 | -4.2** | 99 | 1.6 | 31 | -1.8* | 59 | -1.2 |
| Bonkee (Clintland x PI 185783) | 16.3 | -1.5** | 96 | 2.8** | 32 | 3.2** | 55 | 4.4** |
| Newton x CI 4636 | 19.9 | 2.4** | 93 | 1.5 | 27 | 4.1** | 63 | 13.6** |
| Bonkee (Newton x CI 4636) | 14.3 | -1.6** | 91 | 1.4 | 27 | 3.0** | 45 | -0.3 |
| Clinton x PI 267989 | 17.1 | -3.8** | 98 | 4.3** | 28 | 2.2** | 51 | -1.6 |
| CI 7555 (Clinton x PI 267989) | 16.3 | -2.6** | 98 | 1.1 | 29 | -2.6** | 51 | -5.2** |
| CI 7555$^2$ (Clinton x PI 267989) | 14.5 | -3.3** | 94 | -4.9** | 28 | -6.5** | 46 | -11.7** |
| CI 7555$^3$ (Clinton x PI 267989) | 14.9 | -2.4** | 95 | -4.3** | 30 | -5.8** | 47 | -11.2** |
| CI 7555 x CI 2923 | 22.5 | -7.4** | 95 | -12.4** | 30 | 7.6** | 74 | 4.3** |
| CI 7555$^2$ x CI 2923 | 19.9 | -3.5** | 101 | -3.3** | 35 | 4.5** | 65 | 0.8 |
| CI 7555$^4$ x CI 2923 | 18.4 | -0.1 | 100 | -1.4 | 35 | -0.6 | 62 | 1.3 |
| CI 7555$^6$ x CI 2923 | 17.5 | 0.3 | 99 | -1.8 | 36 | -1.0 | 62 | 2.8 |
| Napped Argent x CI 5545 | 17.5 | -3.0** | 86 | -2.1* | 22 | -0.2 | 48 | 2.5* |
| Goodfield (Napped Argent x CI 5545) | 16.4 | -1.2** | 85 | -0.3 | 22 | -0.8 | 45 | 1.5 |
| Napped Argent x C750 | 20.0 | 0.2 | 91 | -0.5 | 26 | 6.8** | 57 | 12.5** |
| Goodfield (Napped Argent x C750) | 17.6 | 0.4 | 89 | 2.1* | 27 | 5.0** | 51 | 7.9** |
| Goodfield x C750 | 14.4 | -1.2** | 83 | -0.9 | 22 | 2.7** | 39 | 2.1 |

[a]dev=actual-expected mean.

*Actual and expected means differ at .05 level.

**Actual and expected means differ at .01 level.

Table 12 (Continued)

| Cross | Heading date (June) | | Plant height (cm) | | Grain weight (g/plot) | | Straw weight (g/plot) | |
|---|---|---|---|---|---|---|---|---|
| | mean | dev.[a] | mean | dev. | mean | dev. | mean | dev. |
| CI 7970 x CI 5545 | 15.5 | 0.2 | 84 | 1.2 | 23 | 2.5** | 42 | 8.3** |
| CI 7970 x C753 | 14.0 | -0.6 | 85 | -0.8 | 23 | 5.0** | 39 | 6.1** |
| C750 x CI 5545 | 15.0 | -2.3** | 78 | -3.6** | 17 | 1.6* | 33 | 0.8 |
| CI 7970 (C750 x CI 5545) | 14.0 | -1.0** | 81 | -3.1** | 19 | -0.6 | 36 | 2.7* |
| C 237-93 x 13-11 | 16.7 | -9.1** | 89 | -6.4** | 27 | 0.0 | 45 | -10.4** |
| CI 7970 (13-11 x C753) | 16.9 | -1.0** | 91 | 3.3** | 29 | 9.3** | 48 | 9.1** |
| Goodfield x Tippecanoe | 16.1 | 1.4** | 86 | 2.9** | 27 | 1.9** | 46 | 2.1 |
| Newton x CI 7555 | 16.7 | 1.2** | 96 | 2.6* | 31 | 1.1 | 54 | 3.2* |
| Andrew x Burnett | 14.1 | | 95 | | 31 | | 52 | |

deviations from expected means were different for their single crosses. Pusa Hybrid single cross means for heading date were all later than expected, varying from 0.9 days later for Tippecanoe to 1.8 days later for CI 7970. SA 15 single cross means were 2.5 to 4.8 days earlier than expected. Tedere single cross means were 0.4 days later to 1.8 days earlier than expected, although only one deviation was significant. Columbia-Clinton single cross means were 0.2 to 2.5 days earlier than expected, and two of the deviations were significant. Although these cases illustrate the general prepotency of certain exotic and semi-exotic lines for heading date, there were also specific effects as illustrated by the size of the deviations among the single crosses involving a given exotic or semi-exotic variety.

General prepotency of exotic and semi-exotic varieties for grain yield was less frequent. All SA 15 single crosses yielded less than expected, although only two of the deviations were significant. Deviations of mean grain yields from expected values were significant and ranged from 4.0 g less to 1.4 g more than expected for Tedere single crosses. Pusa Hybrid single cross means for grain yield were from 1.4 g less to 1.7 g more than expected, although only the positive deviations were significant. Deviations of Abegweit single cross means included 0.9 and 1.6 g heavier yields and 1.6 g lighter, but only the larger absolute values were significant. None of the Columbia-Clinton single crosses yielded significantly less than expected; deviations were from 1.1 g lighter with CI 7970 to 1.4 and 3.9 g per plot heavier with Goodfield and Tippecanoe, respectively.

There were significant deviations of actual means from expected means for all traits among the adapted x adapted crosses. Four of the crosses headed significantly earlier than expected and two significantly later. Four of the deviations were less than a day, but the Bonham x Clarion cross was 1.0 day earlier and the Clintland x Newton cross was 1.7 days later than expected. Only four of the six adapted x adapted single crosses yielded significantly more or less than expected, but the deviations ranged from 6.5 g lighter for Bonham x Clarion to 4.0 g heavier than expected for Burnett x Cherokee.

Among the three-way crosses involving exotic and semi-exotic varieties, mean heading dates deviated significantly from expected values in 17 of 21 or 81 percent of the crosses (Table 11). Within the groups of three-way crosses, those which involved Tedere, Pusa Hybrid, Columbia-Clinton, and Abegweit had heading dates both earlier and later than expected. All three-way crosses involving SA 15, LMHJ, and Sturdy produced mean heading dates that were earlier than expected. The deviations between actual and expected means were larger for three-way than for single crosses when Tedere, Abegweit, Columbia-Clinton, and Sturdy were involved as parents. Deviations of heading date means for SA 15 three-way crosses were less than for the corresponding single crosses.

In general, it was not possible to predict the deviations between actual and expected heading date means for three-way crosses by knowing the means for related single crosses. Whereas the deviation between the actual and expected heading date means for the cross Tedere x CI 7970 was 1.8 days toward earliness, the mean of CI 7970 (Goodfield x Tedere) was 2.3 days earlier and that of CI 7970 (Tippecanoe x Tedere) was 1.7 days later than expected. No Pusa Hybrid single cross was earlier than expected, but Tippecanoe (Goodfield x Pusa Hybrid) was 1.5 days earlier. The heading date means for the Tippecanoe x Columbia-Clinton crosses were as expected and 2.5 days earlier, respectively, but the mean heading date of the Tippecanoe (CI 7970 x Columbia-Clinton) cross was 3 days later than expected.

For grain yield, two of the 21 three-way cross means, or 10%, were significantly lower than expected, and nine, or 43% were significantly above the expected values. For comparison, six of the 17 single cross means (35%) were significantly below and six were significantly above the expected values. For the single crosses that yielded less and more than expected, the mean deviations were 2.6 and 2.0 g respectively. Corresponding mean deviations for the three-way cross means were 1.6 g less and 3.2 g more. Tedere three-way cross means ranged from 0.5 g less than expected to 4.0 g more for the Goodfield backcross. Also, three-way crosses with Pusa Hybrid yielded from 1.2 g less to 3.9 g more for the CI 7970 (Goodfield x Pusa Hybrid) cross. None of the SA 15 crosses yielded significantly more than expected. CI 7970 (Tippecanoe x Abegweit) yielded 2.5 g more than expected, whereas the largest positive deviation among the Abegweit single crosses was 1.6 g. All of the Columbia-Clinton three-way cross means were significantly higher than expected, ranging from 2.2 g above for CI 7970 (Goodfield x Columbia-Clinton) to 4.3 g above for Tippecanoe (Goodfield x Columbia-Clinton). The mean of the Goodfield (CI 7970 x LMHJ) cross was 1.5 g less than expected.

The unadapted parents used in the crosses tested in 1967 (Table 5) were more genetically divergent from adapted varieties than were those used in 1968 (Table 6). For example, mean heading dates for the unadapted varieties tested in 1967 ranged from June 18 for CI 5545 to July 13 for CI 2923 and five of the seven unadapted varieties had mean heading dates later than June 22. In contrast, in

1968, Tedere, the latest exotic parent, headed on June 21. Therefore, in 1967 there was extended opportunity for environmental influence on productivities of the late parents.

For the single cross, Clintland x PI 185783, the mean heading date was 4.2 days earlier and grain yield was 1.8 g less than expected. When this $F_1$ was crossed to Bonkee, the resulting three-way cross was only 1.5 days earlier than expected, and its mean yield was 3.2 g per plot greater than expected. In actual means, Bonkee caused the three-way cross to be 0.9 days earlier and 1.0 g greater in yield. In actual means, Bonkee caused the three-way cross, Bonkee (Newton x CI 4636), to be 5.6 days earlier than the corresponding single cross, but did not change yield. Data from these pairs of single and three-way crosses support the conclusions from 1968, namely, there was a general improvement in cross means when the percentage of adapted germ plasm was increased.

The crosses involving CI 7555 form an interesting series. The single cross means for Clinton x PI 267989 were 3.8 days earlier and 2.2 g higher in yielding ability than expected. As the backcrossing progressed (Clinton and CI 7555 are isolines), the means for heading date became earlier. The means for $Bc_2$ and $Bc_3$ were actually earlier than either CI 7555 (June 16) or PI 267989 (June 25). The earlier heading dates in the backcrosses could have been caused by linkage of a major gene for early heading date with the gene for rust resistance from PI 267989. Backcrosses were made only on rust resistant plants, and therefore, such a linkage would have perpetuated early heading date for the backcrosses. The mean yields of the backcrosses increased from 28 to 30 g per plot by $Bc_3$, but the deviations between actual and expected yields increased to -6.5 and -5.8 g by $Bc_2$ and $Bc_3$, respectively. Perhaps there was a linkage between rust resistance and a gene(s) for inferior yield also.

In the single cross CI 7555 x CI 2923, the mean heading date was 7.4 days earlier than expected. With repeated back-crossing to $Bc_1$, $Bc_3$, and $Bc_5$ the actual heading date mean regressed toward CI 7555 as expected, and by $Bc_3$ the actual and expected means corresponded closely. The mean yield of the single cross was 7.6 g greater than expected and in the $Bc_1$, $Bc_3$, and $Bc_5$, the mean yields were 35 and 36 g per plot, values that were three to four g greater than for other cross tested in 1967. The mean yield tended to regress toward the CI 7555 parent, but in this series of crosses there was no great improvement in the mean between $Bc_3$ and $Bc_5$.

Napped Argent x CI 5545 was a low yielding single cross (22 g per plot) and the mean heading date was 3.0 days earlier than expected. Crossing this $F_1$ to Goodfield made the mean heading date 1.1 days earlier and failed to change the mean yield. The mean yield for the single cross, Goodfield x C750 was also 22 g, although this was 2.7 g above the expected value. In contrast, Napped Argent x C750 yielded 26 g per plot, which was 6.8 g more than expected, and crossing this $F_1$ to Goodfield improved the mean yield by 1.0 g and made the mean heading date 2.4 days earlier than the single cross. Napped Argent, the highest yielding parent in this series of crosses, yielded 26 g per plot.

C750 x CI 5545, essentially a backcross to the unadapted parent, was the lowest yielding cross (17 g per plot) grown in 1967. Crossing this $F_1$ to CI 7970 increased the yield by 2 g and made the heading date one day earlier. CI 7970 x CI 5545 and CI 7970 x C750 were also low yielding crosses (23 g per plot), although this was 2.5 and 5.0 g respectively, above the expected yields. Deviations of mean heading dates from expected values for these two crosses were not significant. In contrast, CI 7970 (13-11 x C-753) yielded 29 g per plot which was 9.3 g more than expected. The two highest yielding crosses involving CI 5545 germ plasm were similar, complex combinations which could be represented in general, as adapted (unadapted x CI 5545-adapted). The unadapted x CI 5545-adapted portion as represented by Napped Argent x C750 produced the third highest yield of this series of crosses. C 237-93 x 13-11 yielded 27 g per plot, the same as the expected value, but the mean heading date was 9.1 days earlier than expected.

Grain yield means of single crosses tended to be both less and more than expected on the basis of parental performance, and distributed so that the sum of the deviations was near zero. However mean yields of individual single crosses often deviated considerably from expected values, which made the mid-parent values of little use in predicting mean yields of individual crosses. For three-way crosses in 1968, mean yields tended to be greater than expected values. This indicated the value of increasing the proportion of adapted germ plasm upon mean yields. Some of the 1967 data also support this point, but some do not.

## Estimates of Genetic Variability

The presence of genetic variability in a biological population is a requisite for making progress via selection, and the degree of success from selection is, in large part, a reflection of the magnitude of genetic variability present, i.e., a population with the largest genetic variance usually gives the greatest advance from selection. Therefore, I computed the genetic variances for the various oat crosses and summarized them in several ways.

Mean genetic variances for various groups of crosses tested in 1968 and classified on the basis of exotic, semi-exotic, and adapted parents, along with the appropriate standard errors, are given in Table 13. For each trait, the largest mean genetic variance was obtained for adapted x exotic crosses. This result was expected since these crosses represented the hybridization of genetically diverse varieties which leads to high recombination among segregates. The lowest mean genetic variances for all traits except grain yield were obtained for adapted (adapted x semi-exotic) crosses. Mean genetic variances for adapted (adapted x exotic), adapted x semi-exotic, and adapted x adapted crosses were all about equal for grain weight.

In general, if a given exotic or semi-exotic variety imparted high genetic variance to its single crosses, it also produced high (even though reduced) genetic variances in its three-way crosses (Table 14). Among the single crosses, the three exotic parents and Abegweit imparted the highest genetic variances for heading date and plant height, LMHJ, Sturdy, and the exotic parents, imparted the highest genetic variances for grain yield, and the exotic parents and Sturdy for straw yield. Estimates of genetic variances for LMHJ and Sturdy are based on only one cross, so values are less representative than for the exotic and other semi-exotic varieties. Among the three-way crosses, Tedere and Pusa

Table 13. Mean genetic variances and their standard errors for heading date, plant height, grain weight and straw weight by types of crosses tested in 1968

| Type of cross | Number of crosses | Heading date Gen. var. | Heading date Stand. error | Plant height Gen. var. | Plant height Stand. error | Grain weight Gen. var. | Grain weight Stand. error | Straw weight Gen. var. | Straw weight Stand. error |
|---|---|---|---|---|---|---|---|---|---|
| | | (days) | | (cm) | | (g) | | (g) | |
| Adapted x exotic | 9 | 8.1 | 0.6 | 28 | 3 | 30 | 2 | 67 | 6 |
| Adapted (adapted x exotic) | 10 | 5.2 | 0.4 | 19 | 2 | 19 | 2 | 42 | 4 |
| Adapted x semi-exotic | 8 | 4.1 | 0.3 | 21 | 2 | 19 | 2 | 42 | 5 |
| Adapted (adapted x semi-exotic) | 11 | 2.6 | 0.2 | 13 | 1 | 16 | 1 | 36 | 4 |
| Adapted x adapted | 6 | 4.5 | 0.4 | 18 | 2 | 15 | 2 | 48 | 6 |
| All crosses | 44 | 4.8 | 0.2 | 20 | 1 | 20 | 1 | 46 | 2 |

Table 14. Mean genetic variances and their standard errors for heading date, plant height, grain weight and straw weight classified by exotic and semi-exotic parent varieties used in single and three-way crosses tested in 1968

| Single crosses | Number of crosses | Heading date (days) Gen. var. | Stand. error | Plant height (cm) Gen. var. | Stand. error | Grain weight (g) Gen. var. | Stand. error | Straw weight (g) Gen. var. | Stand. error |
|---|---|---|---|---|---|---|---|---|---|
| Tedere | 3 | 7.1 | 0.9 | 25 | 4 | 27 | 4 | 71 | 11 |
| Pusa Hybrid | 3 | 11.2 | 1.4 | 33 | 5 | 31 | 4 | 70 | 11 |
| SA 15 | 3 | 6.0 | 0.8 | 27 | 4 | 32 | 4 | 60 | 10 |
| Abegweit | 3 | 6.8 | 0.9 | 32 | 5 | 21 | 3 | 41 | 8 |
| Columbia-Clinton | 3 | 2.4 | 0.3 | 15 | 3 | 13 | 2 | 30 | 6 |
| LMHJ | 1 | 2.4 | 0.6 | 12 | 4 | 25 | 6 | 51 | 15 |
| Sturdy | 1 | 2.6 | 0.6 | 19 | 6 | 25 | 6 | 71 | 19 |
| Adapted x adapted | 6 | 4.5 | 0.4 | 18 | 2 | 15 | 2 | 48 | 6 |
| Three-way crosses | | | | | | | | | |
| Tedere | 3 | 5.7 | 0.7 | 13 | 3 | 12 | 2 | 46 | 8 |
| Pusa Hybrid | 4 | 6.9 | 0.8 | 26 | 4 | 27 | 3 | 35 | 6 |
| SA 15 | 3 | 2.9 | 0.4 | 17 | 3 | 15 | 2 | 46 | 8 |
| Abegweit | 3 | 2.4 | 0.3 | 18 | 3 | 14 | 2 | 23 | 5 |
| Columbia-Clinton | 4 | 2.6 | 0.3 | 12 | 2 | 11 | 2 | 38 | 6 |
| LMHJ | 2 | 3.0 | 0.5 | 5 | 2 | 18 | 3 | 38 | 9 |
| Sturdy | 2 | 2.7 | 0.5 | 16 | 4 | 26 | 4 | 47 | 10 |

Hybrid, two of the three exotic parents, produced the highest genetic variances for heading date, Pusa Hybrid for plant height, and Pusa Hybrid and Sturdy for grain weight. Abegweit produced the lowest genetic variance among the various groups of three-way crosses for straw weight, and there was little difference among the other groups of three-way crosses for this trait. Columbia-Clinton produced a relatively low genetic variance for all traits in its single crosses, and the mean genetic variance was essentially the same in the single and three-way crosses of this variety.

Genetic variances for individual crosses, from which means for the various groups of crosses were obtained, are shown in Table 15 for single crosses and in Table 16 for three-way crosses grown in 1968. If there were similar magnitudes for variances from all single crosses when a given exotic or semi-exotic parent was crossed to a series of adapted parents, it would be possible to survey a group of exotic varieties for usefulness for expanding genetic variability by making crosses to only one adapted variety. It was shown in the preceding section, however, that deviations of cross means from expected values are rather specific in nature, which indicates that, from the standpoint of cross means, it is more important to find specific combinations of parents that nick favorably than to assay the general value of an exotic line in crosses. Granted, standard errors of the genetic variances for individual crosses were high, but there

Table 15. Genetic variances and their standard errors for heading date, plant height, grain weight, and straw weight for the single crosses tested in 1968

| Cross | Heading date Gen. var. | Heading date Stand. error | Plant height Gen. var. | Plant height Stand. error | Grain weight Gen. var. | Grain weight Stand. error | Straw weight Gen. var. | Straw weight Stand. error |
|---|---|---|---|---|---|---|---|---|
| | (days) | | (cm) | | (g) | | (g) | |
| CI 7970 x Tedere | 5.5 | 1.2 | 28 | 8 | 19 | 5 | 42 | 13 |
| Goodfield x Tedere | 5.3 | 1.2 | 14 | 5 | 29 | 7 | 51 | 15 |
| Tippecanoe x Tedere | 10.6 | 2.3 | 34 | 9 | 33 | 8 | 119 | 29 |
| CI 7970 x Pusa Hybrid | 5.9 | 1.3 | 39 | 10 | 40 | 9 | 49 | 14 |
| Goodfield x Pusa Hybrid | 11.9 | 2.5 | 33 | 9 | 30 | 7 | 73 | 19 |
| Tippecanoe x Pusa Hybrid | 15.8 | 3.3 | 27 | 7 | 23 | 6 | 87 | 22 |
| CI 7970 x SA 15 | 7.4 | 1.6 | 37 | 10 | 52 | 11 | 56 | 16 |
| Goodfield x SA 15 | 5.9 | 1.3 | 27 | 8 | 18 | 5 | 68 | 18 |
| Tippecanoe x SA 15 | 4.6 | 1.0 | 17 | 5 | 25 | 6 | 55 | 16 |
| CI 7970 x Abegweit | 6.6 | 1.4 | 43 | 11 | 23 | 6 | 32 | 11 |
| Goodfield x Abegweit | 4.7 | 1.1 | 32 | 8 | 24 | 6 | 36 | 12 |
| Tippecanoe x Abegweit | 9.1 | 2.0 | 21 | 6 | 16 | 4 | 55 | 16 |
| CI 7970 x Columbia-Clinton | 2.6 | 0.6 | 20 | 6 | 10 | 3 | 22 | 9 |
| Goodfield x Columbia-Clinton | 1.9 | 0.5 | 9 | 4 | 15 | 4 | 21 | 9 |
| Tippecanoe x Columbia-Clinton | 2.6 | 0.6 | 17 | 6 | 14 | 4 | 48 | 14 |

Table 15 (Continued)

| Cross | Heading date Gen. var. | Heading date Stand. error | Plant height Gen. var. | Plant height Stand. error | Grain weight Gen. var. | Grain weight Stand. error | Straw weight Gen. var. | Straw weight Stand. error |
|---|---|---|---|---|---|---|---|---|
| | (days) | | (cm) | | (g) | | (g) | |
| CI 7970 x LMHJ | 2.4 | 0.6 | 12 | 4 | 25 | 6 | 51 | 15 |
| CI 7970 x Sturdy | 2.6 | 0.6 | 19 | 6 | 25 | 6 | 71 | 19 |
| Goodfield Tippecanoe | 2.3 | 0.6 | 8 | 4 | 13 | 4 | 41 | 13 |
| Bonham x Clarion | 3.6 | 0.8 | 18 | 6 | 38 | 9 | 78 | 20 |
| Clintland x Newton | 10.6 | 2.2 | 18 | 6 | 9 | 3 | 73 | 19 |
| Clintland 60 x Marion | 1.9 | 0.5 | 23 | 7 | 3 | 2 | 27 | 10 |
| Burnett x Cherokee | 0.9 | 0.3 | 2 | 2 | 11 | 3 | 30 | 10 |
| Clintland 60 x Beedee | 7.4 | 1.6 | 37 | 10 | 18 | 5 | 36 | 12 |

were some sizeable differences in genetic variances among crosses in groups for most traits (Table 15). For example, among the six adapted x adapted crosses, the genetic variance for grain weight was 38 for the Bonham x Clarion cross and only 3 for the Clintland 60 x Marion cross. In this group, the highest genetic variance for heading date occurred in the Clintland x Newton cross, for plant height in the Clintland 60 x Beedee cross, and for grain and straw weights in the Bonham x Clarion cross.

In general, all single crosses involving Columbia-Clinton produced relatively low genetic variances for all traits, and the differences in genetic variances among the three crosses with this strain were small. The only exception was Tippecanoe x Columbia-Clinton where the straw weight genetic variance was 48 in contrast to 21 and 22 for the other two crosses in this group. The intra-trait genetic variances for the groups of single crosses involving Tedere, Pusa Hybrid, SA 15 and Abegweit were all of about the same magnitude. The only unusually high genetic variance for heading date was 15.8 for Tippecanoe x Pusa Hybrid. Pusa Hybrid crosses tended to show somewhat higher genetic variances for plant height. For straw weight, Abegweit crosses showed somewhat lower genetic variances than did Tedere, SA 15, and Pusa Hybrid.

These data seem to indicate that genetic variances of oat single crosses, just as deviations from expected means, show some general relationship to the exotic or semi-exotic parent used in the cross, but of equal, and perhaps more, importance in determining the magnitude of genetic variance are the specific parents crossed. It is interesting that the range of genetic variances for a trait was almost as great among the adapted x adapted crosses as among all semi-exotic x adapted and exotic x adapted crosses.

As I showed in Table 13, the genetic variances for three-way crosses tested in 1968 were generally reduced from corresponding values for the comparable single crosses. However, there were exceptions to this conclusion, e.g., the grain yield genetic variance for Goodfield (CI 7970 x Pusa Hybrid) was 42 (Table 16), a value that was larger than any comparable genetic variance among the single crosses involving Pusa Hybrid. In the other direction, some genetic variances were extremely small in three-way crosses in comparison with those in corresponding single crosses. For example, the heading date genetic variance for CI 7970 (Goodfield x Tedere) was 0.7 (Table 16), whereas the lowest comparable value for single crosses involving Tedere was 5.3 for Goodfield x Tedere (Table 15). For the three-way crosses (Table 16), the ratios of low to high genetic variances within an exotic or semi-exotic parent group tended to be lower than similar ratios for comparable groups of single

Table 16. Genetic variances and their standard errors for heading date, plant height, grain weight and straw weight for the three-way crosses tested in 1968

| Cross | Heading date Gen. var. | Heading date Stand. error | Plant height Gen. var. | Plant height Stand. error | Grain weight Gen. var. | Grain weight Stand. error | Straw weight Gen. var. | Straw weight Stand. error |
|---|---|---|---|---|---|---|---|---|
| | (days) | | (cm) | | (g) | | (g) | |
| CI 7970 (Goodfield x Tedere) | 0.7 | 0.2 | 4 | 3 | 7 | 2 | 10 | 7 |
| CI 7970 (Tippecanoe x Tedere) | 5.3 | 1.2 | 8 | 4 | 17 | 4 | 66 | 18 |
| Goodfield$^2$ x Tedere | 9.6 | 2.0 | 27 | 7 | 12 | 3 | 62 | 17 |
| CI 7970 (Goodfield x Pusa Hybrid) | 4.4 | 1.0 | 23 | 7 | 14 | 4 | 27 | 10 |
| CI 7970 (Tippecanoe x Pusa Hybrid) | 13.9 | 2.9 | 25 | 7 | 20 | 5 | 47 | 14 |
| Goodfield (CI 7970 x Pusa Hybrid) | 0.9 | 0.3 | 14 | 5 | 42 | 9 | 10 | 7 |
| Tippecanoe (Goodfield x Pusa Hybrid) | 8.5 | 1.8 | 40 | 10 | 34 | 8 | 56 | 16 |
| CI 7970 (Goodfield x SA 15) | 3.0 | 0.7 | 20 | 6 | 16 | 4 | 33 | 11 |
| Goodfield (Tippecanoe x SA 15) | 3.0 | 0.7 | 15 | 5 | 15 | 4 | 52 | 15 |
| Tippecanoe (CI 7970 x SA 15) | 2.6 | 0.6 | 15 | 5 | 15 | 4 | 53 | 15 |
| CI 7970 (Tippecanoe x Abegweit) | 1.8 | 0.5 | 10 | 4 | 10 | 3 | 15 | 7 |
| Goodfield (CI 7970 x Abegweit) | 1.8 | 0.5 | 18 | 6 | 7 | 2 | 15 | 7 |
| Tippecanoe (Goodfield x Abegweit) | 3.7 | 0.8 | 25 | 7 | 24 | 6 | 39 | 12 |

Table 16 (Continued)

| Cross | Heading date Gen. var. | Heading date Stand. error | Plant height Gen. var. | Plant height Stand. error | Grain weight Gen. var. | Grain weight Stand. error | Straw weight Gen. var. | Straw weight Stand. error |
|---|---|---|---|---|---|---|---|---|
| | (days) | | (cm) | | (g) | | (g) | |
| CI 7970 (Goodfield x Columbia-Clinton) | 3.4 | 0.8 | 21 | 6 | 14 | 4 | 24 | 9 |
| Goodfield (CI 7970 x Columbia-Clinton) | 0.8 | 0.3 | 8 | 4 | 6 | 2 | 17 | 8 |
| Tippecanoe (CI 7970 x Columbia-Clinton) | 3.4 | 0.8 | 6 | 3 | 12 | 3 | 82 | 21 |
| Tippecanoe (Goodfield x Columbia-Clinton) | 2.6 | 0.6 | 15 | 5 | 12 | 3 | 29 | 10 |
| Goodfield (CI 7970 x LMHJ) | 2.8 | 0.7 | 6 | 3 | 20 | 5 | 21 | 9 |
| Tippecanoe (CI 7970 x LMHJ) | 3.3 | 0.8 | 5 | 3 | 17 | 4 | 54 | 15 |
| Goodfield (CI 7970 x Sturdy) | 2.8 | 0.7 | 21 | 6 | 31 | 7 | 46 | 14 |
| Tippecanoe (CI 7970 x Sturdy) | 2.6 | 0.6 | 12 | 4 | 20 | 5 | 48 | 14 |

crosses. An exception to this generalization was the SA 15 three-way group, where the ratio was higher for straw weight. Since, generally, mean genetic variances were lower for the groups of three-way crosses, these lower within-group ratios indicated that genetic variances in specific three-way crosses had been reduced significantly. In fact, for the CI 7970 (Goodfield x Tippecanoe) cross, genetic variances were drastically reduced for all traits even when compared to the lowest estimate of genetic variance for each trait among the single crosses with Tedere. On the other hand, the lowest genetic variance for heading date and the highest one for grain yield were found in the same three-way cross, Goodfield (CI 7970 x Pusa Hybrid). These few examples illustrate that no particular magnitude of genetic variance for a trait was associated with the presence of a specific exotic or semi-exotic parent oat variety.

The general reductions in genetic variances found for three-way crosses does not necessarily mean that they have less value for making genetic advance from selection. The reduced genetic variances could be offset by improved means for the three-way crosses, so that the greatest overall genetic advance would result from three-way crosses despite decreased genetic variability. I will discuss this aspect in conjunction with frequency distributions of line means for grain yield.

While genetic variances for the various traits for crosses grown in 1967 support the general conclusion that crosses from diverse parents produce higher genetic variances, the unpredictability of what the genetic variance may be for a specific trait in a specific three-way cross or backcross was also illustrated (Table 17). In both three-way crosses for which Bonkee was the third parent, genetic variance for heading date was reduced materially; for both plant height and grain weight, the genetic variances were similar for the three-way and corresponding single crosses; and for straw weight, genetic variance was increased in one case and reduced in the other. For all traits except plant height, the genetic variances were similar in the single cross Clinton x PI 267989 and the three-way cross, CI 7555 (Clinton x PI 267989). The genetic variances for all traits except grain weight were reduced to about one half for the backcross to CI 7555, but a second backcross failed to further reduce genetic variances. Genetic variances were reduced at near the expected rate for heading date, grain weight, and straw weight in the series of backcrosses involving CI 7555 and CI 2923, but the highest genetic variance for plant height was in the first backcross. Napped Argent and CI 5545 were unadapted varieties and C 750 was a selection from CI 5545 x Burnett (an adapted parent). Relatively high genetic variances were produced by single

Table 17. Genetic variances and their standard errors for heading date, plant height, straw weight and grain weight for the crosses tested in 1967

| Cross | Heading date Gen. var. (days) | Heading date Stand. error (days) | Plant height Gen. var. (cm) | Plant height Stand. error (cm) | Grain weight Gen. var. (g) | Grain weight Stand. error (g) | Grain weight Gen. var. (g) | Grain weight Stand. error (g) |
|---|---|---|---|---|---|---|---|---|
| Clintland x PI 185783 | 11.4 | 2.4 | 32 | 8 | 24 | 6 | 85 | 19 |
| Bonkee (Clintland x PI 185783) | 5.8 | 1.3 | 41 | 10 | 30 | 7 | 116 | 25 |
| Newton x CI 4636 | 13.7 | 2.8 | 16 | 5 | 24 | 6 | 159 | 34 |
| Bonkee x (Newton x CI 4636) | 2.7 | 0.7 | 11 | 4 | 21 | 5 | 30 | 8 |
| Clinton x PI 267989 | 7.4 | 1.8 | 18 | 6 | 40 | 10 | 85 | 21 |
| CI 7555 (Clinton x PI 267989) | 10.4 | 2.2 | 44 | 11 | 44 | 10 | 70 | 16 |
| CI 7555$^{2}$ (Clinton x PI 267989) | 4.1 | 1.0 | 20 | 6 | 30 | 7 | 38 | 10 |
| CI 7555$^{3}$ (Clinton x PI 267989) | 4.2 | 1.0 | 24 | 7 | 34 | 8 | 49 | 12 |
| CI 7555 x CI 2923 | 9.7 | 2.1 | 9 | 4 | 18 | 4 | 99 | 22 |
| CI 7555$^{2}$ x CI 2923 | 4.9 | 1.1 | 31 | 8 | 19 | 5 | 63 | 15 |
| CI 7555$^{4}$ x CI 2923 | 0.4 | 0.3 | 10 | 4 | 6 | 2 | 23 | 7 |
| CI 7555$^{6}$ x CI 2923 | 0.3 | 0.2 | 4 | 3 | 10 | 3 | 31 | 9 |
| Napped Argent x CI 5545 | 11.9 | 2.5 | 55 | 13 | 36 | 8 | 96 | 21 |
| Goodfield (Napped Argent x CI 5545) | 7.1 | 1.6 | 40 | 10 | 27 | 6 | 101 | 22 |
| Napped Argent x C 750 | 10.7 | 2.3 | 24 | 7 | 28 | 8 | 100 | 22 |
| Goodfield (Napped Argent x C 750) | 7.6 | 1.7 | 35 | 9 | 19 | 5 | 64 | 15 |
| Goodfield x C 750 | 6.2 | 1.4 | 37 | 9 | 17 | 4 | 63 | 15 |

Table 17 (Continued)

| Cross | Heading date Gen. var. | Heading date Stand. error | Plant height Gen. var. | Plant height Stand. error | Grain weight Gen. var. | Grain weight Stand. error | Straw weight Gen. var. | Straw weight Stand. error |
|---|---|---|---|---|---|---|---|---|
| | (days) | | (cm) | | (g) | | (g) | |
| CI 7970 x CI 5545 | 5.4 | 1.2 | 30 | 8 | 32 | 7 | 28 | 8 |
| CI 7970 x C 753 | 4.2 | 1.0 | 23 | 6 | 10 | 3 | 31 | 9 |
| C 750 x CI 5545 | 4.2 | 0.9 | 21 | 6 | 9 | 3 | 0 | 0 |
| CI 7970 (C 750 x CI 5545) | 4.9 | 1.1 | 33 | 8 | 22 | 5 | 27 | 8 |
| C 237-93 x 13-11 | 8.0 | 1.7 | 28 | 7 | 24 | 6 | 68 | 16 |
| CI 7970 (13-11 x C 753) | 15.4 | 3.2 | 27 | 7 | 23 | 5 | 130 | 28 |
| Goodfield x Tippecanoe | 3.5 | 0.8 | 18 | 5 | 15 | 4 | 43 | 11 |
| CI 7555 x Newton | 7.8 | 1.9 | 24 | 7 | 21 | 6 | 66 | 17 |
| Andrew x Burnett | 0.0 | 0.0 | 8 | 4 | 6 | 3 | 18 | 7 |

crosses of Napped Argent with CI 5545 and C 750. The three-way cross involving Goodfield with Napped Argent x CI 5545, which would have only half adapted germ plasm, produced somewhat reduced genetic variances for three traits. Goodfield (Napped Argent x C 750) and Goodfield x C 750 produced similar genetic variances for all traits. C 237-93 and CI 7970, selections from the same cross, produced similar genetic variances for plant height and grain weight in C 237-93 x 13-11 and CI 7970 (13-11 x C 753), but the three-way cross produced higher genetic variances for heading date and straw weight.

Genetic variances for the various traits in the adapted by adapted crosses, when compared to unadapted x adapted crosses, ranged from moderate magnitude for CI 7555 x Newton to low for Goodfield x Tippecanoe to very low for Andrew x Burnett.

In summary, genetic variances were, on the average, greater for crosses involving relatively diverse varieties. Also, genetic variances for three-way crosses and backcrosses tended to be lower than for corresponding single crosses. Generally, if the genetic variances were high for single crosses involving an exotic or semi-exotic variety, genetic variances in three-way crosses or backcrosses with the same variety were also relatively high. However, for a specific three-way or backcross genetic variances were unpredictable from corresponding single cross behavior.

### Distribution of Line Means in Relation to Performance of Adapted Varieties for Heading Date, Plant Height, and Grain and Straw Weight

Means and genetic variances are convenient for summarizing data from biological populations, but selection is practiced on the basis of individual line means, and whether or not a line is kept depends upon its means relative to the means of other lines in the population and to check varieties for a number of traits. The required performance levels for some traits may be, simply, that they fall within certain limits that are defined by the range of means for this trait among adapted varieties. Sometimes the mean of a line needs to be near one limit, or even outside, of the range, when a plant breeder believes such a performance level will improve the crop variety, or fit the variety for some specific situation, i.e., earliness might allow double cropping, short plants are associated with lodging resistance, and heavy straw yield would be desirable for forage production. The highest possible grain yield is a usual goal, as long as a line meets the established standards for other traits.

In summarizing my data, I have shown the percentage of line means that fall within the range of the adapted varieties I tested, and percentages that fall above and below this range, in Table 18 for 1968 crosses and Table 19 for 1967 crosses, for heading date, plant height and straw weight. The limits for the ranges were set by the ranges of check variety and adapted parent means in the two experiments (Tables 5, 6, and 7).

For 1968, only Tedere produced a significant percentage of lines that would be eliminated because of excessively late heading dates (10% in the single crosses and 6% in the three-way crosses). Single crosses with Pusa Hybrid (51%), SA 15 (33%), LMHJ (21%), and Sturdy (15%) produced significant numbers of lines which headed earlier than June 12, as did Pusa Hybrid three-way crosses (31%). Tedere and adapted x adapted groups of single crosses produced 15 and 10%, respectively, of lines taller than 92.0 cm, the upper limit for the check varieties, and Pusa Hybrid single crosses produced 38%, and for its three-way crosses 10% of lines shorter than 71.5 cm. For straw weight, Columbia-Clinton three-way crosses had 11%, and the adapted x adapted crosses had 7% of lines that produced more straw than the upper limit of the checks, whereas all groups of crosses except Columbia-Clinton single and three-way crosses, Sturdy single crosses, and LMHJ three-way crosses had more than 10% of lines for which straw weight was less than the

Table 18. Percentages of line means above, within, and below the range of means of adapted varieties for heading date, plant height, and straw weight by groups of single crosses and three way crosses with exotic, semi-exotic and adapted parents (1968)

| | Heading Date | | | Plant Height | | | Straw Weight | | |
|---|---|---|---|---|---|---|---|---|---|
| | Earlier than Je 12 | Je 12-Je 20.5 | Later than Je 20.5 | Shorter than 71.5 cm | 71.5-92.0 cm | Taller than 92.0 cm | Less than 45.1 g | 45.1-75.0g | More than 75.0g |
| Tedere single crosses | 2 | 88 | 10 | 0 | 85 | 15 | 31 | 68 | 1 |
| Tedere three-way crosses | 2 | 92 | 6 | 0 | 98 | 2 | 25 | 74 | 1 |
| Pusa Hybrid single crosses | 51 | 49 | 1 | 38 | 62 | 0 | 62 | 38 | 1 |
| Pusa Hybrid three-way crosses | 31 | 68 | 0.5 | 10 | 89 | 1 | 40 | 60 | 0 |
| SA 15 single crosses | 33 | 67 | 1 | 4 | 94 | 1 | 11 | 86 | 3 |
| SA 15 three-way crosses | 10 | 90 | 0 | 6 | 94 | 0 | 18 | 81 | 1 |
| Abegweit single | 8 | 90 | 2 | 5 | 91 | 4 | 16 | 83 | 1 |
| Abegweit three-way crosses | 9 | 91 | 0 | 2 | 97 | 1 | 13 | 87 | 0 |
| Columbia-Clinton single crosses | 6 | 94 | 0 | 0 | 99 | 1 | 6 | 92 | 3 |
| Columbia-Clinton three-way crosses | 2 | 96 | 2 | 0 | 97 | 3 | 2 | 87 | 11 |
| LMHJ single crosses | 21 | 79 | 0 | 0 | 100 | 0 | 25 | 75 | 0 |
| LMHJ three-way crosses | 10 | 90 | 0 | 1 | 99 | 0 | 10 | 86 | 3 |

Table 18 (Continued)

| | Heading Date | | | Plant Height | | | Straw Weight | | |
|---|---|---|---|---|---|---|---|---|---|
| | Earlier than Je 12 | Je 12- Je 20.5 | Later than Je 20.5 | Shorter than 71.5 cm | 71.5- 92.0 cm | Taller than 92.0 cm | Less than 45.1g | 45.1- 75.0g | More than 75.0g |
| Sturdy single crosses | 15 | 85 | 0 | 4 | 96 | 0 | 0 | 96 | 2 |
| Sturdy three-way crosses | 10 | 90 | 0 | 9 | 91 | 0 | 16 | 84 | 0 |
| Adapted x adapted | 0.3 | 96 | 3 | 0.3 | 90 | 10 | 1 | 92 | 7 |

Table 19. Percentages of line means above, within, and below the range of means of adapted varieties for heading date, plant height, and straw weight for crosses tested in 1967

| Cross | Heading Date | | | Plant Height | | | Straw Weight | | |
|---|---|---|---|---|---|---|---|---|---|
| | Earlier than Je 12 | Je 12- Je 20.5 | Later than Je 20.5 | Shorter than 78.5 cm | 78.5- 106 cm | Taller than 106 cm | Less than 35.1g | 35.1- 60g | More than 60g |
| Clintland x PI 187783 | 2 | 82 | 16 | 0 | 92 | 8 | 0 | 58 | 42 |
| Bonkee (Clintland x PI 185783) | 4 | 94 | 2 | 0 | 94 | 6 | 4 | 66 | 30 |
| Newton x CI 4636 | 0 | 44 | 56 | 0 | 98 | 2 | 4 | 66 | 30 |
| Bonkee (Newton x CI 4636) | 10 | 90 | 0 | 2 | 98 | 0 | 4 | 94 | 2 |
| Clinton x PI 267989 | 3 | 85 | 13 | 0 | 98 | 2 | 0 | 66 | 14 |
| CI 7555 (Clinton x PI 267989) | 12 | 80 | 8 | 2 | 86 | 12 | 0 | 80 | 20 |
| CI $7555^2$ (Clinton x PI 267989) | 10 | 90 | 0 | 0 | 100 | 0 | 6 | 92 | 2 |
| CI $7555^3$ (Clinton x PI 267989 | 4 | 96 | 0 | 0 | 100 | 0 | 2 | 98 | 0 |
| CI 7555 x CI 2923 | 0 | 36 | 64 | 0 | 98 | 2 | 0 | 8 | 92 |
| CI $7555^2$ x CI 2923 | 0 | 76 | 24 | 0 | 84 | 16 | 0 | 30 | 70 |
| CI $7555^4$ x CI 2923 | 0 | 98 | 2 | 0 | 92 | 8 | 0 | 40 | 60 |
| CI $7555^6$ x CI 2923 | 0 | 100 | 0 | 0 | 100 | 0 | 0 | 36 | 64 |
| Napped Argent x CI 5545 | 4 | 76 | 20 | 22 | 78 | 0 | 6 | 78 | 16 |

Table 19 (Continued)

| Cross | Earlier than Je 12 | Je 12-Je 20.5 | Later than Je 20.5 | Shorter than 78.5 cm | 78.5-106 cm | Taller than 106 cm | Less than 35.1g | 35.1-60g | More than 60g |
|---|---|---|---|---|---|---|---|---|---|
| Goodfield (Napped Argent x CI 5545) | 6 | 90 | 4 | 16 | 84 | 0 | 28 | 68 | 4 |
| Napped Argent x C 750 | 0 | 68 | 32 | 0 | 100 | 0 | 0 | 60 | 40 |
| Goodfield (Napped Argent x C 750) | 0 | 92 | 8 | 6 | 94 | 0 | 0 | 90 | 10 |
| Goodfield x C 750 | 18 | 82 | 0 | 28 | 72 | 0 | 38 | 60 | 2 |
| CI 7970 x CI 5545 | 6 | 92 | 2 | 22 | 78 | 0 | 14 | 86 | 0 |
| CI 7970 x C 753 | 14 | 86 | 0 | 10 | 90 | 0 | 32 | 66 | 2 |
| C 750 x CI 5545 | 6 | 94 | 0 | 54 | 46 | 0 | 72 | 28 | 0 |
| CI 7970 (C 750 x CI 5545) | 16 | 84 | 0 | 32 | 68 | 0 | 44 | 56 | 0 |
| C 237-93 x 13-11 | 0 | 90 | 10 | 2 | 96 | 2 | 12 | 84 | 4 |
| CI 7970 (13-11 x C 753) | 0 | 90 | 10 | 32 | 68 | 0 | 8 | 80 | 8 |
| Goodfield x Tippecanoe | 4 | 96 | 0 | 4 | 96 | 0 | 2 | 94 | 4 |
| CI 7555 x Newton | 0 | 95 | 5 | 0 | 98 | 2 | 3 | 78 | 20 |
| Andrew x Burnett | 0 | 100 | 0 | 0 | 100 | 0 | 0 | 90 | 10 |

lower limit of adapted varieties. The relatively large number of lines with lower straw weight than adapted varieties probably was in part due to the low straw yield of CI 7970, Goodfield, and Tippecanoe which were the adapted parents used in the crosses with the exotic and semi-exotic varieties.

In 1967, many lines with late heading dates were expected because several of the unadapted parents were late in maturity. In all single crosses where a large percentage of lines were later than the latest adapted variety, crossing it into a three-way cross or backcross materially increased the percentage of lines falling within the range of the adapted varieties. For the single cross with PI 185783, the percentage of late lines was 16, but only 2 for the three-way cross; for the single and three-way crosses the percentages of late lines were 56 and 0, respectively, with CI 4636, 13 and 8, respectively, with PI 267989, 64 and 24, respectively, with CI 2923, and 20 and 4, and 32 and 8, respectively, for the crosses involving Napped Argent. Few lines headed earlier than June 12.

Only crosses involving CI 5545, C 750, and C 753 (the latter two parents are selections from CI 5545 x adapted crosses) produced significant numbers of lines that were shorter than the lower limit of adapted varieties, but the mean plant height for CI 5545 was only 78 cm. Two crosses with CI 7555, a tall (100 cm) adapted parent produced crosses in which more than 10% of the lines were taller than 106 cm. The crosses with CI 7970, CI 5545, C 750, and C 753 produced relatively large percentages of lines with low straw weight which reflected the low straw yield characteristic of these parents. Note that 72 percent of the lines from the single cross C 750 x CI 5545 produced less than 35 g of straw. CI 7555 had a straw yield near the upper limit (59 g per plot) of the adapted parent range and CI 2923 yielded 80 g of straw, with the result that large percentages of lines from crosses involving these two parents produced very high straw yields (60% to 94% of the lines in the crosses of these two parents yielded more than 60 g of straw per plot). The range of straw yields for the adapted varieties was rather narrow in 1967, and this was a factor in the number of lines that fell outside the range of adapted varieties.

In summary, distributions of the means of oat lines for heading date, plant height and straw weight, as expected, were related to the magnitudes of these traits for the parents of the various crosses. In general, increasing the proportion of adapted germ plasm, through backcrossing and making three-way crosses, which involved two adapted parent varieties, effectively increased the percentage of lines that fell within the range of adapted parents for these traits.

In the previous section, I have shown that three-way and backcrosses to adapted parent varieties were effective in increasing the percentage of lines that fell within the range of adapted varieties for heading date, plant height, and straw weight. The same effect was found, in a general way, for yield. I have illustrated this in Table 20, which shows

Table 20. Percentages of line means for grain yield above, below, and within the range of 21.1 to 27.0 g per plot for single and three-way crosses arranged by exotic or semi-exotic parents and tested in 1968

| Type of cross and exotic or semi-exotic parent | Less than 21.1 g | 21.1 to 27.0 g | More than 27.0 g |
|---|---|---|---|
| Tedere single crosses | 53 | 31 | 15 |
| Tedere three-way crosses | 18 | 47 | 35 |
| Pusa Hybrid single crosses | 69 | 24 | 7 |
| Pusa Hybrid three-way crosses | 42 | 35 | 23 |
| SA 15 single crosses | 16 | 40 | 44 |
| SA 15 three-way crosses | 15 | 45 | 40 |
| Abegweit single crosses | 13 | 39 | 49 |
| Abegweit three-way crosses | 8 | 40 | 51 |
| Columbia-Clinton single crosses | 3 | 25 | 72 |
| Columbia-Clinton three-way crosses | 2 | 27 | 72 |
| LMHJ single cross | 15 | 50 | 35 |
| LMHJ three-way crosses | 17 | 36 | 47 |
| Sturdy single cross | 19 | 44 | 38 |
| Sturdy three-way crosses | 22 | 31 | 47 |
| Goodfield x Tippecanoe | 8 | 33 | 58 |

the percentage of lines that fall within, above, and below a range of 21.1 to 27.0 g per plot for single and three-way crosses grouped according to exotic and semi-exotic parent and tested in 1968. The distribution of lines from the adapted cross, Goodfield x Tippecanoe, was included for comparison. The range from 21.1 to 27.0 g per plot represented the yield extremes of the three adapted parents used in the adapted x exotic and adapted x semi-exotic crosses.

For Tedere and Pusa Hybrid, mean grain yield was greater for three-way crosses than for single crosses, and this is reflected by a smaller percentage of low grain-yielding lines (i.e., below 21.1 g per plot) in the three-way crosses from these varieties than in their corresponding single crosses. Of course, these results are typical of what would be expected with very wide crosses where the exotic parent would be low yielding. In my experiment, only Tedere and Pusa Hybrid were real low in yield. SA 15 and all of the semi-exotic varieties yielded more grain than Tippecanoe (i.e., 26 g per plot), the highest yielding adapted variety involved in crosses with exotic and semi-exotic varieties in the 1968 experiment (Table 6). The mean yield of SA 15 three-way crosses was less than that of its single crosses, but line means were similarly distributed above, within, and below the adapted variety range for both types of crosses. Within both Abegweit and Columbia-Clinton, the corresponding three-way and single crosses produced very similar distributions of grain yields. The largest change was a reduction from 13 to 8% in the proportion of lines yielding less than 21.1 g per plot for Abegweit three-way crosses. For LMHJ and Sturdy a complete set of single crosses was not grown, but the high yielding class (i.e. above 27.0 g per plot) contained a substantially larger percentage of lines from the three-way crosses than from the corresponding single crosses. The percentage of lines falling within the range of 21.1 to 27.0 g per plot ranged from 24% for Pusa Hybrid single crosses to 50% for the CI 7970 x LMHJ single cross, and the corresponding percentage for the Goodfield x Tippecanoe single cross was 33. The 58% of high yielding lines in the Goodfield x Tippecanoe cross was exceeded only by the single and three-way crosses to Columbia-Clinton. These frequency distributions for grain yield were closely related to the means for the groups of crosses, and since the means for several groups of crosses were near 27 g per plot, having approximately 50% of the lines of a distribution above this level, was an expected result.

To this point, I have described the effects of segregation from single and three-way crosses of oats in terms of general statistics, i.e., means, genetic variances, and frequency distributions. However, in the real world of plant breeding for grain yield, the value of a cross is judged on the basis of its production of lines that yield better than the highest yielding parent, and more realistically, better than the best available commercial varieties.

To relate to this point, I have shown in Table 21, for the crosses tested in 1968, the number of lines that exceeded the yield of the high parent, the number of lines that exceeded the yield of the high parent by 5 g per plot (5 g per plot was the least significant difference for comparing a line mean with the mean of a parent), and the yield of the highest yielding line in each cross.

All single crosses segregated some lines with mean yields greater than the yield of the high parent in the cross. However two of the adapted by adapted crosses, Bonham x Clarion and Clintland 60 x Marion, two Pusa Hybrid single crosses, Goodfield x SA 15, and two Columbia-Clinton single crosses failed to produce a line with a mean yield 5 g above the high parent. As a group, the Pusa Hybrid single crosses had low mean yields (probably due to germ plasm of Pusa Hybrid which yielded only 10 g per plot). They produced a small proportion of lines that were higher yielding than the better parents, and when judged against yields of the best commercial varieties, the 28.8 to 30.0 g yields for the best segregates were not encouraging. Among the SA 15 single crosses, Goodfield x SA 15 produced few superior yielding lines, and the best one was not significantly better than the higher yielding parent variety. On the

Table 21. Numbers of lines yielding more grain than higher yielding parent, number of lines and yield of highest yielding segregate for crosses tested in 1968

| | Number of lines yielding more than higher parent | Number of lines yielding 5g more than higher parent | Mean yield of highest yielding line |
|---|---|---|---|
| CI 7970 x Tedere | 7 | 2 | 32.2 |
| Goodfield x Tedere | 10 | 3 | 36.2 |
| Tippecanoe x Tedere | 24 | 9 | 37.4 |
| CI 7970 x Pusa Hybrid | 11 | 0 | 29.6 |
| Goodfield x Pusa Hybrid | 11 | 3 | 30.0 |
| Tippecanoe x Pusa Hybrid | 2 | 0 | 28.8 |
| CI 7970 x SA 15 | 17 | 8 | 44.4 |
| Goodfield x SA 15 | 3 | 0 | 36.2 |
| Tippecanoe x SA 15 | 10 | 3 | 38.8 |
| CI 7970 x Abegweit | 26 | 6 | 38.6 |
| Goodfield x Abegweit | 8 | 2 | 39.6 |
| Tippecanoe x Abegweit | 19 | 7 | 40.4 |
| CI 7970 x Columbia-Clinton | 6 | 0 | 36.4 |
| Goodfield x Columbia-Clinton | 11 | 0 | 36.6 |
| Tippecanoe x Columbia-Clinton. | 31 | 4 | 42.2 |
| CI 7970 x LMHJ | 3 | 2 | 39.4 |
| CI 7970 x Sturdy | 9 | 9 | 38.6 |
| Goodfield x Tippecanoe | 29 | 11 | 35.8 |
| Bonham x Clarion | 2 | 0 | 44.8 |
| Clintland x Newton | 27 | 2 | 34.8 |
| Clintland 60 x Marion | 6 | 0 | 37.8 |
| Burnett x Cherokee | 11 | 3 | 47.4 |
| Clintland 60 x Beedee | 17 | 5 | 42.0 |
| CI 7970 (Goodfield x Tedere) | 15 | 0 | 29.2 |
| CI 7970 (Tippecanoe x Tedere) | 22 | 8 | 32.8 |
| Goodfield x Tedere | 40 | 18 | 35.4 |

Table 21 (Continued)

| | Number of lines yielding more than higher parent | Number of lines yielding 5g more than higher parent | Mean yield of highest yielding line |
|---|---|---|---|
| CI 7970 (Goodfield x Pusa Hybrid) | 22 | 3 | 37.2 |
| CI 7970 (Tippecanoe x Pusa Hybrid) | 7 | 0 | 30.0 |
| Goodfield (CI 7970 x Pusa Hybrid) | 21 | 2 | 32.4 |
| Tippecanoe (Goodfield x Pusa Hybrid) | 7 | 5 | 37.2 |
| CI 7970 (Goodfield x SA 15) | 8 | 0 | 35.6 |
| Goodfield (Tippecanoe x SA 15) | 3 | 0 | 35.2 |
| Tippecanoe (CI 7970 x SA 15) | 5 | 0 | 36.4 |
| CI 7970 (Tippecanoe x Abegweit) | 31 | 5 | 36.2 |
| Goodfield (CI 7970 x Abegweit) | 5 | 0 | 33.6 |
| Tippecanoe (Goodfield x Abegweit) | 22 | 7 | 41.4 |
| CI 7970 (Goodfield x Columbia-Clinton) | 10 | 3 | 39.2 |
| Goodfield (CI 7970 x Columbia-Clinton) | 4 | 1 | 37.2 |
| Tippecanoe (CI 7970 x Columbia-Clinton) | 22 | 2 | 40.8 |
| Tippecanoe (Goodfield x Columbia-Clinton) | 18 | 4 | 40.0 |
| Goodfield (CI 7970 x LMHJ) | 2 | 0 | 36.8 |
| Tippecanoe (CI 7970 x LMHJ) | 10 | 1 | 38.8 |
| Goodfield (CI 7970 x Sturdy) | 19 | 7 | 38.4 |
| Tippecanoe (CI 7970 x Sturdy) | 28 | 8 | 36.2 |

other hand, CI 7970 x SA 15 and Tippecanoe x SA 15 segregated eight and three lines, respectively, that were significantly superior to the higher yielding parent. Note that the highest yielding line (44.4 g per plot) from all single crosses of exotic and semi-exotic with adapted varieties, occurred in the CI 7970 x SA 15 cross. The Columbia-Clinton single crosses produced from few (six in CI 7970 x Columbia-Clinton) to many (31 in Tippecanoe x Columbia-Clinton) lines that were higher yielding than the better parents, but only the latter cross segregated lines that were significantly superior to the better parent. Surprisingly (since Tedere was a relatively low yielding variety at 23 g per plot), the Tedere single crosses produced reasonable numbers of lines that yielded more grain than the better parent (seven for CI 7970 x Tedere to 24 for Tippecanoe x Tedere), and also, reasonable numbers of lines that were significantly superior to the better parent (two for CI 7970 x Tedere to nine for Tippecanoe x Tedere). Abegweit single crosses also segregated a relatively large number of lines that were both higher yielding and significantly higher yielding than the better parents.

Among the adapted x adapted crosses, Bonham x Clarion and Clintland 60 x Marion failed to produce any lines that yielded 5 g above the higher parent. The mean yield for the Bonham x Clarion cross was 7 g less than the expected value, but the genetic variance for grain yield for this cross was the highest of all the adapted x adapted crosses. The failure of the Clintland 60 x Marion cross to produce significantly superior lines resulted from an extremely low genetic variance of only 3.0. The largest difference between parental means for an adapted x adapted cross was 13 g between Burnett and Cherokee. The mean yield for this cross was 4 g above the expected value, but the genetic variance was only average. Of course, the highest yielding line segregated from any cross was from Burnett x Cherokee (47.4 g per plot).

Generally, all single crosses, whether of adapted x adapted, adapted x exotic, or adapted x semi-exotic parentage, segregated lines that were higher yielding than the better parents, and a majority of the single crosses, 17 of 23, produced lines that were significantly superior to the better parents in the crosses. There were considerable differences among single crosses with a common exotic or semi-exotic parent, relative to all three criteria used to summarize crosses in Table 21, namely, number of lines that yielded more than better parents, number of lines that were significantly superior to the better yielding parent, and grain yield of the best line. Of course, the same was true for the adapted x adapted crosses. In the final analysis the two highest yielding lines, at 47.4 and 44.8 g per plot, were segregated from the adapted x adapted crosses, i.e., Burnett x Cherokee and Bonham x Clarion, respectively.

The mean yields of Tedere three-way crosses were higher than those of Tedere single crosses, and the number of lines yielding above the higher parent was increased from 41 to 77, and the number of lines yielding 5 g above the higher parent was increased from 14 to 26. However, the grain yields of the highest yielding lines generally were lower for the three-way than for the corresponding single crosses. Similarly, making three-way crosses where Pusa Hybrid was a parent increased the cross yield means and the number of lines that yielded more grain than the better parents. Also, the yield of the best line was materially better in the three-way crosses (37.2 g per plot) than in the single crosses (30.0 g per plot). One Tedere and one Pusa Hybrid three-way cross failed to produce any lines that yielded 5 g more than the higher parent. Generally, making three-way crosses with SA 15 as a parent tended to depress the segregation of high yielding lines when compared to SA 15 single crosses. No SA 15 three-way cross produced lines that yielded 5 g above the higher parent, and the highest yielding line among the single crosses (44.4 g per plot in CI 7970 x SA 15) was significantly higher (at .01 level) than the highest yielding line in the three-way crosses (36.4 g per plot in Tippecanoe (CI 7970 x SA 15)). Segregation for grain yield was similar in single and three-way crosses involving Abegweit. The numbers of lines that yielded either more, or significantly more, than the higher yielding parents were similar. However, the highest yielding line (41.4 g per plot) was produced from the three-way cross, Tippecanoe (Goodfield x Abegweit). The yield of this line was not significantly different from the highest yielding line (40.4 g per plot) from the single crosses. Also, the Columbia-Clinton single and three-way crosses were quite equivalent in producing high yielding lines. The highest yielding line (42.2 g per plot) was produced by a single cross (Tippecanoe x Columbia-Clinton), but its yield was not significantly different from the highest yielding lines of any of the other Columbia-Clinton crosses. Two of the highest yielding lines of the three-way crosses yielded 40.8 and 40.0 g per plot. None of the single or three-way crosses involving LMHJ produced many lines that yielded 5 g more than the higher parent, whereas all crosses involving the Sturdy variety produced a reasonable number of lines that yielded significantly superior to the higher parent. Of course, the comparisons for LMHJ and Sturdy were not as complete as those for Tedere, Pusa Hybrid, SA 15, Abegweit, and Columbia-Clinton.

In the 1968 experiment, as expected, the inclusion of an additional adapted parent into a three-way cross, by crossing an adapted parent to a single cross which had an exotic or semi-exotic parent, tended to drag the three-way cross toward mediocrity for yield. For Pusa Hybrid, three-way crosses tended to be better for yield than single crosses, but single crosses with this parent were notably poor. For crosses with Tedere, SA 15, Columbia-Clinton, LMHJ, and Sturdy, the three-way and single crosses with a common exotic or semi-exotic parent produced about equivalent numbers of lines that were significantly superior to the better parents, but for each of these exotic or semi-exotic parent varieties, the highest yielding segregate came from a single cross.

All of the crosses grown in 1967 (Table 22), for which parental values were available for comparison, produced at least one line which yielded 5 g per plot more than the higher parent, except C 750 x CI 5545. The three-way cross of Bonkee to Clintland x PI 185783 produced an increased mean for yield, and caused an increase in the number of lines that yielded more (23 and 16 lines) and significantly more (seven and four lines) than the higher yielding parent. The highest yielding line from the three-way cross yielded significantly more (47.2 vs 40.7 g per plot) than the highest yielding line from the single cross. In contrast, the cross of Bonkee with Newton x CI 4636 caused a general reduction in superior yielding segregates and a 5.4 g reduction in yield of the highest producing line from the single cross.

The means and variances of the series of crosses, Clinton x PI 267989 through CI $7555^3$ (Clinton x PI 267989),

Table 22. Number of lines yielding more grain than higher yielding parent, number of lines yielding 5 g more, and yield of highest yielding segregate for crosses tested in 1967

| | Number of lines yielding more than higher parent | Number of lines yielding 5g more than higher parent | Mean yield of highest yielding line (g) |
|---|---|---|---|
| Clintland x PI 185783 | 16 | 4 | 40.7 |
| Bonkee (Clintland x PI 185783) | 23 | 7 | 47.2 |
| Newton x CI 4636 | 36 | 9 | 44.7 |
| Bonkee (Newton x CI 4636) | 32 | 16 | 39.3 |
| Clinton x PI 267989 | 3 | 1 | 45.0 |
| CI 7555 (Clinton x PI 267989) | 6 | 1 | 43.3 |
| CI $7555^2$ (Clinton x PI 267989) | 3 | 1 | 43.5 |
| CI $7555^3$ (Clinton x PI 267989) | 7 | 2 | 50.0 |
| CI 7555 x CI 2923 | 4 | 1 | 42.5 |
| CI $7555^2$ x CI 2923 | 10 | 4 | 47.3 |
| CI $7555^4$ x CI 2923 | 5 | 1 | 46.3 |
| CI $7555^6$ x CI 2923 | 17 | 4 | 44.7 |
| Napped Argent x CI 5545 | 11 | 6 | 36.7 |
| Goodfield (Napped Argent x CI 5545) | 14 | 5 | 33.0 |
| Napped Argent x C 750 | 24 | 14 | 40.8 |
| Goodfield (Napped Argent x C 750) | 29 | 9 | 39.7 |
| Goodfield x C 750 | 14 | 4 | 34.5 |
| CI 7970 x CI 5545 | 28 | 9 | 36.7 |
| CI 7970 x C 753 | 24 | 6 | 30.2 |
| C 750 x CI 5545 | 23 | 0 | 22.8 |
| CI 7970 (C 750 x CI 5545) | 9 | 2 | 28.5 |
| C 237-93 x 13-11 | 7 | 1 | 38.7 |
| CI 7970 (13-11 x C 753) | 43 | 28 | 41.3 |
| Goodfield x Tippecanoe | 28 | 9 | 35.5 |
| CI 7555 x Newton | 4 | 1 | 42.7 |
| Andrew x Burnett | | | 37.7 |

were similar, as were the numbers of lines that yielded more than CI 7555 (the higher yielding parent), and the number of lines that yielded significantly more than CI 7555. The highest yielding line produced in the CI $7555^3$ (Clinton x PI 267989) cross yielded significantly more than the highest yielding line in any of the other crosses involving these parents. In the backcrossing series, CI 7555 x CI 2923 through CI $7555^6$ x CI 2923, the mean yield was progressively increased and the numbers of lines yielding above CI 7555 tended to increase, but the number of lines yielding significantly above CI 7555 was not changed greatly (from one to four). The highest yielding line was found in the first backcross, but it was not significantly superior to corresponding lines from the other crosses involving these two parent varieties. CI 2923 yielded poorly in this test, probably because its grain filling had not been completed before the experiment was harvested. This could explain transgressive segregation in spite of a low genetic variance.

Napped Argent was the highest yielding variety in the series of crosses involving it as a parent with CI 5545, C 750 and Goodfield (Table 5). The numbers of lines yielding more than the high parent, lines yielding 5.0 g more than the high parent, cross means, and genetic variances were similar for the single cross, Napped Argent x CI 5545 and the three-way cross, Goodfield (Napped Argent x CI 5545). The best line from the single cross (36.7 g per plot) was higher in yield than the best one from the three-way cross (33.0 g per plot), but not significantly so. The single cross, Napped Argent x C 750 produced 14 lines that yielded significantly above the higher parent, and its best segregate yielded 40.8 g per plot. When Goodfield was crossed with Napped Argent x C 750 to give a three-way cross, the number of lines that yielded significantly more than the higher parent was decreased to nine and the yield of the best line was only 39.7 g per plot. Compared to Goodfield (Napped Argent x C 750), the yields of the cross Goodfield x C 750 and the best lines from it were reduced. CI 7970 x CI 5545 and CI 7970 x C 753 produced similar numbers of lines that were superior and significantly superior to the higher parent, but the highest producing line from CI 7970 x CI 5545 yielded 6.5 g more than its counterpart from the CI 7970 x C 753 cross. C 750 x CI 5545 was a very poor cross. CI 7970 x CI 5545, CI 7970 x C 753, and CI 7970 (C 750 x CI 5545) represent combinations with expectations of 50, 25, and 37.5% CI 5545 germ plasm. The highest yielding line came from the cross with the highest percentage of CI 5545 germ plasm. The mean yield of the higher parent was 11.0 g less (Table 5) in the CI 7970 (13-11 x C 753) cross than in the C 237-93 x 13-11 cross which resulted in a larger number of lines yielding more than the best parent in the three-way cross.

The yield of the best line from the Goodfield x Tippecanoe cross was not materially different from comparable lines from other crosses involving Goodfield with unadapted parents. The yield of the best line from the Newton x CI 7555 was 42.7 g per plot, but this was lower than the best lines from Bonkee (PI 185783 x Clintland), Newton x CI 4636, all crosses involving CI 7555, Clinton and PI 267989, and the backcrosses involving CI 7555 and CI 2923.

In summary, while the proportion of line means for grain yield within the range of adapted varieties was increased and the percentage of line means yielding more, or even significantly more, than the highest yielding parent tended to be increased, especially where the adapted parents were the higher yielding varieties, the best yielding lines from three-way and backcrosses usually were not significantly different from the highest yielding lines from the corresponding single crosses. This would mean that where exotic varieties were used as parents, the use of backcrosses or three-way crosses would be logical as a method for increasing the percentage of lines that would meet acceptable standards for other agronomic traits, especially if the exotic or unadapted variety was quite divergent phenotypically. If the unadapted variety was quite similar to the adapted variety in most agronomic traits, a single cross probably would provide as much transgressive segregation for yield as would any other type of cross and therefore, three-way or back-crossing would not be necessary.

### Relationship of Cross Means and Genetic Variances to Yield of Best Segregate

Cross means and variances and yields of the highest yielding segregates from each cross are summarized in Tables 23 and 24 for 1968 and 1967, respectively. This summary permits inspection of relationships among the three statistics. High means and high variances should increase the probability of high yielding segregates, whereas low means could counteract high variances, etc.

Now, the highest yielding line in the 48 to 50-line sample from a cross was only 2% of the sample, and if 2% was the true frequency of this particular line in the population, there was a 96% probability that it would not be included even if two 50-line samples were drawn from the population. In addition, the standard error of a line mean was relatively high, which means that the actual yield of the most favorable genotype could have varied considerably. However, the highest yielding segregate from a group of crosses generally came from the cross with the highest mean and/or genetic variance.

The highest yielding segregate from Tedere single crosses was from the cross with the highest mean and variance, as was true,also,for the SA 15 single crosses. The highest yielding

Table 23. Means and genetic variances for grain yield for the crosses tested in 1968 and means of highest yielding segregate from each cross

| Single crosses | Cross mean | Genetic variance | Mean of highest line |
|---|---|---|---|
| CI 7970 x Tedere | 21 | 19 ± 5 | 32.2 |
| Goodfield x Tedere | 19 | 29 ± 7 | 36.2 |
| Tippecanoe x Tedere | 26 | 33 ± 8 | 37.4 |
| CI 7970 x Pusa Hybrid | 19 | 40 ± 9 | 29.6 |
| Goodfield x Pusa Hybrid | 18 | 30 ± 7 | 30.0 |
| Tippecanoe x Pusa Hybrid | 16 | 23 ± 6 | 28.8 |
| CI 7970 x SA 15 | 28 | 52 ± 11 | 44.4 |
| Goodfield x SA 15 | 26 | 18 ± 5 | 36.2 |
| Tippecanoe x SA 15 | 27 | 25 ± 6 | 38.8 |
| CI 7970 x Abegweit | 29 | 23 ± 6 | 38.6 |
| Goodfield x Abegweit | 26 | 24 ± 6 | 39.6 |
| Tippecanoe x Abegweit | 28 | 16 ± 4 | 40.4 |
| CI 7970 x Columbia-Clinton | 28 | 10 ± 3 | 36.4 |
| Goodfield x Columbia-Clinton | 29 | 15 ± 4 | 36.6 |
| Tippecanoe x Columbia-Clinton | 33 | 14 ± 4 | 42.2 |
| CI 7079 x LMHJ | 25 | 25 ± 6 | 39.4 |
| CI 7970 x Sturdy | 26 | 25 ± 6 | 38.6 |
| Goodfield x Tippecanoe | 27 | 13 ± 4 | 35.8 |
| Bonham x Clarion | 30 | 38 ± 9 | 44.8 |
| Clintland x Newton | 29 | 9 ± 3 | 34.8 |
| Clintland 60 x Marion | 32 | 3 ± 2 | 37.8 |
| Burnett x Cherokee | 37 | 11 ± 3 | 47.4 |
| Clintland 60 x Beedee | 30 | 18 ± 5 | 42.0 |

Table 23 (Continued)

| Three-way crosses | Cross mean | Genetic variance | Mean of highest line |
|---|---|---|---|
| CI 7970 (Goodfield x Tedere) | 24 | 7 ± 2 | 29.2 |
| CI 7970 (Tippecanoe x Tedere) | 26 | 17 ± 4 | 32.8 |
| Goodfield$^2$ x Tedere | 27 | 12 ± 3 | 35.4 |
| CI 7970 (Goodfield x Pusa Hybrid) | 25 | 14 ± 4 | 37.2 |
| CI 7970 (Tippecanoe x Pusa Hybrid) | 20 | 20 ± 5 | 30.0 |
| Goodfield (CI 7970 x Pusa Hybrid) | 23 | 42 ± 9 | 32.4 |
| Tippecanoe (Goodfield x Pusa Hybrid) | 21 | 34 ± 8 | 37.2 |
| CI 7970 (Goodfield x SA 15) | 27 | 16 ± 4 | 35.6 |
| Goodfield (Tippecanoe x SA 15) | 24 | 15 ± 4 | 35.2 |
| Tippecanoe (CI 7970 x SA 15) | 27 | 15 ± 4 | 36.4 |
| CI 7970 (Tippecanoe x Abegweit) | 29 | 10 ± 3 | 36.2 |
| Goodfield (CI 7970 x Abegweit | 25 | 7 ± 2 | 33.6 |
| Tippecanoe (Goodfield x Abegweit) | 28 | 24 ± 6 | 41.4 |
| CI 7970 (Goodfield x Columbia-Clinton) | 29 | 14 ± 4 | 39.2 |
| Goodfield (CI 7970 x Columbia-Clinton) | 28 | 6 ± 2 | 37.2 |
| Tippecanoe (CI 7970 x Columbia-Clinton) | 31 | 12 ± 3 | 40.8 |
| Tippecanoe (Goodfield x Columbia-Clinton) | 31 | 12 ± 3 | 40.0 |
| Goodfield (CI 7970 x LMHJ) | 24 | 20 ± 5 | 36.8 |
| Tippecanoe (CI 7970 x LMHJ) | 29 | 17 ± 4 | 38.8 |
| Goodfield (CI 7970 x Sturdy) | 25 | 31 ± 7 | 38.4 |
| Tippecanoe (CI 7970 x Sturdy) | 27 | 20 ± 5 | 36.2 |

Table 24. Means and genetic variances for grain yield for crosses tested in 1967 and mean of highest yielding segregate from each cross

| | Cross mean | Genetic variance | Mean of highest yielding line |
|---|---|---|---|
| Clintland x PI 185783 | 31 | 24 ± 6 | 40.7 |
| Bonkee (Clintland x PI 185783) | 32 | 30 ± 7 | 47.2 |
| Newton x CI 4636 | 27 | 24 ± 6 | 44.7 |
| Bonkee (Newton x CI 4636) | 27 | 21 ± 5 | 39.3 |
| Clinton x PI 267989 | 28 | 40 ± 10 | 45.0 |
| CI 7555 (Clinton x PI 267989) | 29 | 44 ± 10 | 43.3 |
| CI $7555^2$ (Clinton x PI 267989) | 28 | 30 ± 7 | 43.5 |
| CI $7555^3$ (Clinton x PI 267989) | 30 | 34 ± 8 | 50.0 |
| CI 7555 x CI 2923 | 30 | 18 ± 4 | 42.5 |
| CI $7555^2$ x CI 2923 | 35 | 19 ± 5 | 47.3 |
| CI $7555^4$ x CI 2923 | 35 | 6 ± 2 | 46.3 |
| CI $7555^6$ x CI 2923 | 36 | 10 ± 3 | 44.7 |
| Napped Argent x CI 5545 | 22 | 36 ± 8 | 36.7 |
| Goodfield (Napped Argent CI 5545) | 22 | 27 ± 6 | 33.0 |
| Napped Argent x C 750 | 26 | 28 ± 8 | 40.8 |
| Goodfield (Napped Argent x C 750) | 27 | 19 ± 5 | 39.7 |
| Goodfield x C 750 | 22 | 17 ± 4 | 34.5 |
| CI 7970 x CI 5545 | 23 | 32 ± 7 | 36.7 |
| CI 7970 x C 753 | 23 | 10 ± 3 | 30.2 |
| C 750 x CI 5545 | 17 | 9 ± 3 | 22.8 |
| CI 7970 (C 750 x CI 5545) | 19 | 22 ± 5 | 28.5 |
| C 237-93 x 13-11 | 27 | 24 ± 6 | 38.7 |
| CI 7970 (13-11 x C 753) | 29 | 23 ± 5 | 41.3 |
| Goodfield x Tippecanoe | 27 | 15 ± 4 | 35.5 |
| CI 7555 x Newton | 31 | 21 ± 6 | 42.7 |
| Andrew x Burnett | 31 | 6 ± 3 | 37.7 |

segregates from all Pusa Hybrid single crosses yielded similarly, as did those from Abegweit single crosses, although there were differences among means and variances within each set of single crosses. Variances of the Columbia-Clinton single crosses were similar, but the highest yielding segregate was produced by the cross with the highest mean. The two highest yielding segregates among the adapted by adapted crosses were produced from the cross with the highest mean (Burnett x Cherokee) and the cross with the highest variance (Bonham x Clarion).

Among Tedere three-way crosses, the lowest and highest among the best yielding transgressive segregates were produced by the crosses with the lowest and highest means, respectively. Among Pusa Hybrid three-way crosses, two lines were highest yielding with 37.2 g per plot, and they were produced by the cross with the highest mean and the cross with second highest variance. The highest yielding segregates from SA 15 three-way crosses differed little in spite of a 3 g difference in cross means, and the highest yielding segregate from the Abegweit three-way crosses came from the cross with the greatest variance. The genetic variances of all Columbia-Clinton three-way crosses were similar, and the highest yielding lines, at 40.8 and 40.0 g per plot were from the crosses with the highest means. For LMHJ and Sturdy three-way crosses highest yielding segregates were associated with the highest cross mean and highest cross genetic variance, respectively.

In general, for these oat crosses, the highest yielding segregate was associated with a high cross mean, a high cross genetic variance, or both, even though there was no precise quantitative relationship. The lack of a precise relationship was not surprising in view of the relatively large errors associated with line mean and genetic variance estimates.

In 1967 also, there was a general relationship between high means and/or genetic variances for a cross and the yield of the highest yielding segregate. The mean yield and genetic variance for Bonkee (Clintland x PI 185783) were slightly higher than for the corresponding single cross, and the mean of the highest yielding line from the three-way cross was 6.5 g higher than the mean of the highest yielding line from the single cross. There was no difference in the mean of Newton x CI 4636 and the three-way cross of this $F_1$ crossed to Bonkee, but the genetic variance of the single cross was higher, and the yield of the best line from the single cross exceeded the yield of the best segregate from the three-way cross by 5.4 g. The highest yielding segregate from the crosses involving PI 267989 was produced by CI 7555[3] (Clinton x PI 267989) which had the highest mean, and of the crosses involving CI 2923, the highest yielding line was produced by the first backcross which had relatively high mean and genetic variance.

Of the five crosses involving Napped Argent, CI 5545, C 750 and Goodfield, the two crosses with superior means produced best segregates. The cross of CI 7970 x CI 5545, produced a higher genetic variance than CI 7970 x C 753, C 750 x CI 5545, and CI 7970 (C 750 x CI 5545), and a higher mean than the latter two crosses. The yield of its best segregate was 6.5 g greater than the yield of any segregate from the other three crosses. C 237-93 x 13-11 and CI 7970 (13-11 x C 753) had similar variances, but the mean yield of the three-way cross was 2 g higher and it produced the highest yielding segregate.

The highest yielding segregate from the adapted x adapted crosses grown in 1967 was produced by CI 7555 x Newton. The mean yield of this cross was the same as that of Andrew x Burnett and its genetic variance was the highest in the group.

These results show the importance of both a high cross mean and a high genetic variance for crosses to produce high yielding segregates.

# DISCUSSION OF RESULTS AND CONCLUSIONS

There were two points about my experiments which could have biased somewhat the magnitudes of mean and variance estimates obtained. First, I used random lines from parent varieties for testing rather than using lines established from the specific parent plants involved in the crosses. I did find significant genetic variances among lines within several of the parental varieties. The progenies from specific parent plants were not saved separately when the original crosses were made, so I had no alternative to using random lines. Second, since each of my experiments was conducted at only one location and for only one year, the effects of genotype x environment interaction on mean and variance estimates could not be determined. If the experiments had been grown in more than one environment fewer crosses could have been sampled, so I chose to use more crosses and only one experiment for each.

In calculating the expected mean for a particular single, three-way or backcross, I used the parental variety means in proportion to their expected contributions of germ plasm to the cross. For example, the expected mean for the Pusa Hybrid x Goodfield single cross was the mid-parent value, and for the Tippecanoe (Goodfield x Pusa Hybrid) three-way cross, the expected value was 1/2 Tippecanoe mean + 1/4 Goodfield mean + 1/4 Pusa Hybrid mean. This type of calculation was based on the assumption of additive gene action only, which may or may not have been a correct assumption. As shown earlier, many of the cross means did deviate considerably from the expected values.

Now these deviations of cross means could have been caused by any one, or various combinations, of several factors. Dominance, epistasis, linkage, and non-random selection of lines could have been factors that could cause such deviations in single cross means. In three-way and backcrosses, limited sampling of gametes from $F_1$ plants used as parents could have caused deviations also.

My oat lines were tested in $F_4$, so dominance should have been of relatively little importance as a type of gene action affecting the performance of quantitative traits. Of course, if the heterozygote had a strong selective advantage, it should not have affected the number of $F_2$-derived lines I used, but it could have led to a high proportion of heterozygous plants within lines. Any extent to which such a factor operated could have biased my estimates of cross means. Very likely, dominant gene action was not a significant contributor to deviations of actual from expected cross means. After all, since CI 7970, Goodfield and Tippecanoe were closely related (Table 3), heterozygosity and dominance probably should have been of less importance in the three-way than in the single crosses, but the greatest general trend for deviations occurred in the three-way crosses tested in 1968.

The resultant effects of crossing over or breaking up of blocks of genes from the exotic parent varieties would likely be greater and more permanent in three-way and backcrosses to adapted varieties than in single crosses of exotic x adapted varieties. Certainly, a portion of the crossing over that occurred in the $F_1$ of a single cross could be negated by subsequent reverse crossing over in the same chromosome region in later generations of selfing. In contrast, particular crossovers would essentially be fixed in three-way, and especially in backcrosses, with little opportunity for reversal. This line of reasoning is made in the general sense of adapted vs. exotic as two general pools of germ plasm. Actually, this phenomenon might affect the potentiality a cross would have for segregating extreme segregates more than it might affect the cross mean.

The effects of epistasis can be illustrated by the probabilities associated with reconstituting a favorable epistatic combination present in an adapted parent from single crosses and backcrosses (assuming the epistatic combination is due to two independently inherited loci). If the effect of a gene from an adapted parent can be expressed only when associated with another independent gene from the same parent, only 25% of the pure line segregates from a single cross with exotic or semi-exotic lines would benefit from such an allele, whereas 56% of the pure lines from a backcross would do so. This illustrates how restoring a greater proportion of a base of adapted germplasm could increase the means of three-way or backcrosses relative to corresponding single crosses. Of course, a gene from an exotic parent could complement one from the adapted parent to improve progeny performance, but this would be expected less frequently than two genes from an adapted parent complementing each other.

Natural selection should operate similarly upon single and three-way crosses, so probably it would not cause differential expression of means for single and three-way crosses.

When three-way or backcrosses are made in oats, the usual number of seeds obtained is from six to 20, which means that a like number of gametes is used from the $F_1$ used in the back- or three-way crossing. Therefore, the sample of gametes from an $F_1$ plant used in three-way or backcrosses, certainly could not be representative of the complete possible array. Obviously, this factor could be important in the unpredictability of variances and means of three-way or backcrosses. However, if inadequate sampling occurred randomly, three-way cross means should be depressed as often as improved, unless some force such as natural selection eliminated "poor gametes" from the sample.

Of the possible factors which could explain the higher-than-expected means for three-way crosses, restoration of favorable gene combinations from adapted parents, and breakup of linkages from unadapted germ plasm would seem to be the most logical ones.

The introgression of germ plasm from exotic oat lines into germplasm pool of adapted varieties, would seem to have potential for yield improvement as demonstrated by the relatively common occurrence of transgressive segregates for high yield in the crosses tested in my study. In 1968, the potentiality for transgressive segregates for high grain yield from exotic and semi-exotic x adapted crosses that were superior to high yielding segregates from adapted x adapted crosses, was limited because the adapted parents used in my exotic x adapted crosses were low yielding varieties, CI 7970, Tippecanoe and Goodfield. Among the parents of the adapted x adapted crosses, other than the Goodfield x Tippecanoe cross, only Newton yielded as little as 26 gm per plot (Table 6). The yields of CI 7970, Tippecanoe and Goodfield were only 26, 26 and 23 gm per plot respectively. In spite of this low level of yield for the adapted parents, the highest yielding segregate from an adapted x adapted cross yielded only 3 gm per plot more than the highest yielding segregate from an adapted x exotic cross. In 1967, when higher yielding adapted parents were involved in adapted x unadapted crosses, the highest yielding segregates were produced by such crosses. In addition, the infusion of alleles from exotic or semi-exotic varieties should contribute to high genetic variability when the best yielding lines from the exotic x adapted crosses are used in a second cycle of crossing and selection.

The general conclusions, that I have reached from this study are: 1) Deviations of actual cross means, for the different traits, from the means expected on the basis of parental performance were sufficiently frequent, and of sufficient magnitude, to indicate that non-additive gene action, presumably epistasis, was of some importance in significantly affecting performance of crosses between specific parents. 2) Improved cross performance for yield, when measured as deviations from expected performance, was frequently found for three-way crosses and backcrosses relative to corresponding single crosses. 3) Parental performance was a sufficiently reliable estimator of cross progeny performance to permit planning of single, three-way, and backcrosses to permit adjustment of means so that a large percentage of lines would meet accepted standards for many agronomic traits, with the result that selection of lines that combined superior yield with acceptable levels of other agronomic traits would be enhanced in three-way and backcrosses over single crosses. 4) Genetic variance was greater, on the average, for relatively wide single crosses. Whereas the changes in genetic variance from single to three-way and backcrosses was unpredictable for specific related parental combinations, high genetic variance in single crosses tended to carry over, on the average, into related three-way and backcrosses. This relationship, also, would operate to permit a planned series of crosses for introgressing germ plasm from exotic parents into standard varieties. 5) A three-way or backcross which improved the mean over a related cross for a given trait also tended to increase the number of positive transgressive segregates for that trait. Of course, in a specific cross, a large reduction in genetic variance sometimes offset the benefit of the improved mean. For yield, however, the difference between the means of the highest yielding segregates from a single cross and a corresponding three-way or backcross were usually not significant, even though genetic variances and means for the two crosses showed considerable change.

# SUMMARY

Actual means of oat crosses frequently deviated from means expected on the basis of parental performance for heading date, plant height, and grain and straw yield. For heading date, single cross means reflected prepotencies of exotic and semi-exotic parents when averaged over the group of single crosses with each parent, but the magnitudes of deviations among single crosses with a common exotic or semi-exotic parent indicated specific interactions between the adapted and exotic or semi-exotic parents. Larger deviations were generally found for specific three-way than for specific single crosses, but when averaged over a group, the three-way cross deviation was usually smaller than the average deviation for single crosses.

Grain yields for single crosses of adapted with exotic or semi-exotic parents tended to be inferior to expected values, more often than did the grain yields of comparable three-way crosses. In fact, 6, 5, and 6 actual single cross means were inferior, the same as, and superior to expected values, respectively, whereas for three-way crosses, 2, 10, and 9 means were inferior, the same as, and superior, respectively, to expected values.

Genetic variances were highest for crosses with the most diverse parentage but there were large differences among genetic variances within a group of single crosses with a given

exotic parent crossed to different adapted varieties. If a given exotic parent imparted high genetic variance to its single-crosses, genetic variances of its three-way crosses were also relatively high. Single cross variances were not especially useful for predicting the variances of a corresponding three-way cross.

Crosses of genetically divergent parents tended to produce large percentages of lines that fell outside the range of adapted varieties, and use of an adapted parent in a three-way or backcross tended to increase the percentage of lines that fell within this range. Usually, the highest yielding segregates were obtained from the cross or crosses in an exotic parent group, which had the highest mean and/or genetic variance.

Exotic and semi-exotic oat varieties seemed to have potential for improving yield of adapted varieties. Although the adapted parents involved in crosses with exotic and semi-exotic varieties in 1968 were low yielding, the highest yielding segregates for yield from these crosses compared favorably with the highest yielding segregates from adapted x adapted crosses. In 1967, when higher yielding adapted parents were involved in crosses with unadapted varieties the highest yielding segregates were invariably produced by these crosses.

Dominance, epistasis, non-random selection, and linkage were discussed as possible causes of deviations of actual from expected cross means, unpredictability of variances, and the relatively better yield of three-way over single crosses. Restoration of favorable epistatic gene combinations common to adapted varieties seemed to be most logical for explaining the better relative yielding ability of the three-way crosses.

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